The African Penguin *Spheniscus demersus*: Conservation and Management Issues

by

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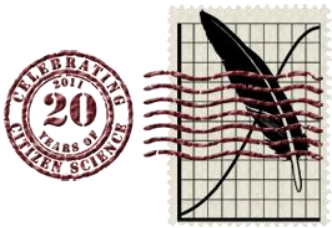

Declaration

I hereby declare that all the work presented in this thesis, titled "The African Penguin *Spheniscus demersus*: Conservation and Management Issues", is my own, except where otherwise stated in the text. This thesis has not been submitted in whole or in part for a degree at any other university.

Signed in Cape Town in February 2011

……

Lauren Jane Waller

To Mom and Dad.

For your unconditional love, support, belief and encouragement;

for all you've done and sacrificed for us, I love you so much.

This is for you.

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ABSTRACT

Title: The African penguin *Spheniscus demersus*: conservation and management issues

Author: Lauren Jane Waller

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The African penguin is a southern African endemic, with its breeding distribution within the Benguela Upwelling Ecosystem. The IUCN conservation status of this species was re-classified from 'Vulnerable' to 'Endangered' in 2010. This thesis investigated some aspects pertinent to the species' conservation and management.

Time series of population estimates of African penguins and fish biomass were available in South Africa since the late 1980s. This study analysed the fish biomass at a stratum scale, which is a finer scale to that of previous studies which looked at biomass estimates as a whole. The strata range in length from c. 155 km to c. 280 km in length. The number of African penguin breeders and adult moulters were found to be positively correlated with fish biomass estimates, although results of the spatial relationships were unexpected. The islands which displayed the strongest relationships were Dassen Island and Robben Island. These islands are only c. 50 km apart, and it is expected that they would experience similar oceanographic conditions. However, the colonies at these islands were found to respond differently to fish biomass estimates. While the number of Dassen Island birds were found to be positively correlated with biomass estimates within the strata in which the island is found, the number of Robben Island birds were correlated with biomass estimates of the stratum to the south and east of the island. Weaker relationships were found for the remaining colonies. This study suggested that the period of moult is of critical importance to the survival of the penguin, an aspect that needs to be incorporated into the Ecosystem Approach to Fisheries modelling.

Moult patterns and seasonality were reviewed for Namibia and South Africa. Colonies at South Africa displayed more synchronous moult seasonality than that of colonies in Namibia. The ratio of moulters to breeders suggested that there is substantial movement of birds from breeding colonies to other locations in which to

moult, giving further evidence of differences in local prey availability. Dyer Island was the colony at which adult moult was most synchronous of all colonies studied, and also had the most frequent incidence of end of season orphan chicks compared to other colonies. The rapidly declining number of breeders and moulters at all colonies, despite this evidence of movement by moulters, suggested significant mortality, which is likely to take place at sea.

A chick condition index was used to compare the condition of African penguin chicks on five South African colonies from 2008 and 2009, using chick condition in 2004 as a baseline reference level. Chick condition was found to vary through the year so that an annual condition index needs to be based on data collected throughout the breeding season, and not on a single sampling occasion. African penguin chicks were generally in a poorer condition in 2009 than in 2008. Chicks at Dyer Island had consistently poorer condition than chicks at other breeding colonies.

The foraging behaviour of breeding African penguins was investigated in 2008, 2009 and 2010. There was no significant difference between foraging and diving parameters between the years, suggesting feeding conditions were similar throughout the course of the study. In 2010, penguins foraged in a different area to that of 2008 and 2009. In comparison with previous studies of African penguin foraging behaviour, birds from Dyer Island tended to have longer foraging trip durations, travelled farther distances, with larger foraging ranges than that of penguins at other colonies.

Finally, the legislative context within South Africa for the protection of this species was discussed. The National Environmental Management: Biodiversity Act (No. 10 of 2004) provides a mechanism to incorporate all aspects of African penguin conservation with its provision for the compilation of a 'Biodiversity Management Plan for Species.' This Act is drawn up within the principles of co-operative governance, providing a platform for the variety of government departments involved in aspects that deal with issues relating to the African penguin, to contribute to a single, unified Management Plan. Furthermore, the management plan needs to be based on sound science, and provides a mechanism for scientists to engage with policy makers to ensure that the most up to date conservation science recommendations are included in the plan.

LAYOUT AND CONTRIBUTION OF CO-AUTHORS

This thesis consists of five main chapters, each written as a paper for submission to a journal. As a result, some repetition, particularly in the introduction was inevitable. Tables and figures follow the text for each chapter, as would be done in a paper submitted for publication. The references are included at the end of each chapter. Professor Les Underhill commented on all drafts, and provided assistance with data analysis.

CHAPTER 2: The estimates of pelagic fish biomass were obtained from Dr Janet Coetzee, Department of Agriculture, Forestry and Fisheries. African penguin count data were obtained from Prof Rob Crawford, Department of Environmental Affairs. Together with CapeNature staff, I conducted the moult and breeding census counts at Dyer Island from 2007. Dr Lynne Shannon and Prof Rob Crawford commented on a draft of the chapter.

CHAPTER 3: The Namibian moult counts and penguin breeding numbers were obtained from Dr Jessica Kemper. The South African penguin data were obtained from Prof Rob Crawford, Department of Environmental Affairs. Together with CapeNature staff, I conducted the moult and breeding census counts at Dyer Island from 2007. Dr Jessica Kemper commented on a draft of the chapter.

CHAPTER 4: The chick condition data were collected as part of the DEA Fisheries closure project. I was responsible for all data collection on Dyer Island. Robben Island data were obtained from Johan Visagie and Leshia Visagie at Dassen Island; Dr Richard Sherley and Dr Nola Parsons at Robben Island; Dr Lorien Pichegru at St Croix Island and Bird Island. Namibian data were supplied by Dr Jessica Kemper and Dr Katta Ludynia. Dr Jessica Kemper commented on a draft of the chapter. The data used to provide the baseline information for the condition index were supplied by Sandra Bouwhuis. The condition index itself was developed by Alwyn Lubbe as part of a BSc(Hons) project.

CHAPTER 5: I was responsible for the collection of penguin foraging data at Dyer Island for 2008, 2009 and 2010. Dr Lorien Pichegru processed the raw data through MT–Dive. Dr Rene Navarro analysed the data through a DRS script that he devised

for his PhD. Further analyses were conducted by myself. Dr Katta Ludynia and Dr Rene Navarro commented on earlier drafts of the chapter.

CHAPTER 6: I formed part of a team that organised an African penguin workshop in October 2010, the aim of which was to identify threats and mitigating measures that would provide the baseline information for the compilation of the draft Biodiversity Management Plan for the African penguin for submission to the Minister of Department of Environmental Affairs. One of my roles was to summarise and interpret the biodiversity conservation legislation in South Africa that pertained to the African penguin. This chapter was commented on by Coral Birss, Kevin Shaw and Magdel Boshoff.

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I never dreamed I would ever contemplate, let alone register and work on a PhD, and it has been an enriching time in my life. Fortunately, there is no 'I' in PhD, and the 'P' could be for 'people' since so many people have been part of this study and contributed in such a variety of ways. As I've been compiling my acknowledgements over the last few weeks, I've been so humbled to see the number of people I can thank, who've seen fit to invest in me and this project, it would not have been possible without you all. It has been a privilege to have been able to do this study, and I am so grateful to a number of people who have participated through financial contributions, assistance with fieldwork, provided friendship, support and encouragement, and in their many different ways, enabled this project to come to fruition.

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To Deon Geldenhuys, Conservation Manager at Dyer Island and 'technical advisor.' Thank you so much for your interest in this project and for your constant assistance with field work, especially during the penguin tracking season, breeding surveys, and chick condition. I would not have been able to do this project without you. Your skill in navigating Osprey back to Kleinbaai at night when fieldwork finished late, and during high seas in winter never had me question our safety at sea. You sacrificed so much of your own time to make sure the data that was needed was collected, so much of which still needs to be worked on after this project is completed. Thank you for the cooking lessons on the island while waiting for loggers to come back, it will however take me another thesis to figure out how to get my bread to rise evenly on the Dyer Island stove, surely it's the stove and not me? Thank you for cheerfully making sure we finished the fieldwork on days when the weather was cold wet and windy. Thank you for your friendship, for sharing a passion for seabirds, islands and their conservation, I hope I can support you as much as you've been there for me in your future studies.

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Many days of fieldwork on the island involved keeping half a (weary) eye on abalone poachers around the island. The staff house was eventually broken into in 2010, and I'm grateful for the swift response of the (then) MCM (now DAFF) law enforcement and Gansbaai police to come and collect us in the middle of the night. This incident resulted in Swift tern chicks being trampled by the poachers and sadly, abalone poaching continues around Dyer and other islands along South Africa's coastline.

My interest in conservation, particularly in the marine and coastal field started at a very young age. Teachers at school picked up on my interest and steered me in various directions to develop it. I'm particularly thankful to Mrs Venter for this. My interest was also fuelled by the environmental education programme we had at

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To dad and mom, where do I even start without having first to swallow two rugby ball sized lumps in my throat, one for each of you. I love you so much. I know you would have loved to have been more involved in this project, making food, walking Diesel and washing windows;-) You can see from the list above however, I've had wonderful people around me. Thank you for instilling in kleinboet and I a love for the outdoors at such an early age, and for family holidays by the sea and in the mountains. You've sacrificed so much for us. This is for you.

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To Dyer Island and African penguins. My hope is that in some small way, what comes out of this project will be of benefit to you.

To The One, I'm in awe of You.

CHAPTER 1

INTRODUCTION

Photo: D Geldenhuys

A string of offshore islands are scattered along the coast of South Africa and Namibia. The southernmost, c. 60 km from Cape Agulhas, is Dyer Island. Conservation issues at Dyer Island are the primary focus of this thesis. These issues are considered in context, so the "parish" of this thesis extends beyond Dyer Island to include aspects of the Benguela Upwelling Ecosystem, and the biodiversity and administration of the region, as appropriate. This introduction establishes the general framework for the chapters that follow.

Benguela Upwelling Ecosystem

The Benguela Upwelling Ecosystem is one of four major eastern boundary current systems in the southern hemisphere (Hill *et al*. 1998) and extends from Algoa Bay, adjacent to Port Elizabeth on South Africa's south coast to the Angola Front on the west coast of Namibia (Figure 1, Figure 2) (Schwartzlose *et al*. 1999). This ecosystem is one of the most productive areas of ocean in the world (Brown *et al*. 1991). It is characterised by coastal wind-induced upwelling which results in cold, nutrient rich-water being transported to the surface (Shannon 1985). This upwelled water is the basis for the high biological productivity of the coastal waters along the west coast of southern Africa and is a rich feeding ground of a number of marine species (Shannon 1989, van der Lingen *et al*. 2006). In addition to its productivity, it is also extremely dynamic, showing great variability across a range of temporal scales (Field and Shillington 2004, van der Lingen *et al*. 2006).

The South Atlantic high pressure system dominates this upwelling system and determines the prevailing winds. The austral summer (October–March) is characterised by strong southeasterly winds that drive the upwelling process, with the upwelling intensity reaching a maximum in January (Lehodey *et al*. 2006). These southerly winds peak in three locations in the Bengeula; at Cape Point, Lüderitz and Cape Frio (Figure 1) (Hutchings *et al*. 2009b). Conversely, cyclonic low pressure systems passing south of the continent in winter, are accompanied by northwesterly winds that push surface waters onshore, resulting in reduced upwelling (Lehodey *et al*. 2006).

The Benguela Upwelling Ecosystem is divided into the northern and southern regions, with the boundary generally taken at the Orange River estuary, between South Africa and Namibia (Shannon 1989). I will refer to them as the northern Benguela and southern Benguela. The Benguela Upwelling Ecosystem contains a number of upwelling cells in areas where the wind is strongest and continental shelf narrowest (Shannon

1989), with the Lüderitz upwelling cell in the northern Benguela the largest single upwelling centre (Shannon 1985). The northern Benguela extends from the Angola-Benguela front, south to Lüderitz (Figure 1) (van der Lingen *et al*. 2006). The upwelled water is cold as a result of the cold Benguela Current and cold water from the ocean depths which are brought to the surface by the prevailing strong longshore southerly and southwesterly winds (Shannon 1989). The intense upwelling cells transport nutrient-rich water to the surface, and as this water is warmed and oxygenated, phytoplankton and zooplankton utilise these nutrients (Wearne and Underhill 2005), providing a food source to the upper trophic levels such as pelagic fish. It is in this region that the Namibian Islands and penguin breeding colonies are situated (Figure 2) (Kemper 2006). The powerful upwelling cell at Lüderitz separates the northern and southern Benguela regions and the turbulence associated with this upwelling acts as an environmental barrier between the two regions for marine organisms (van der Lingen *et al*. 2006, Hutchings *et al*. 2009b).

The southern Benguela lies off the west coast of South Africa. It extends from the Lüderitz upwelling cell to the Agulhas Bank off South Africa's south coast (van der Lingen *et al*. 2006) (Figure 1). It is a highly variable system due in part to strong southerly winds around the Cape Peninsula causing an accelerated and pronounced upwelling effect. These winds are characterised by strong short-term patterns in the prevailing wind direction, resulting in rapid changes in upwelling intensity (Shannon 1985, Lehodey *et al*. 2006).

In the northern Benguela, there is a tendency for phytoplankton and winds to peak in late winter-spring, and in summer and autumn in the southern Benguela, thus showing opposite seasonal signals (Hutchings *et al*. 2009b). These upwelling systems are important determinants for the pelagic fish off southern Africa and the implications of this for marine top predators, particularly African penguins *Spheniscus demersus* is described in further detail in Chapter 2.

Seabird assemblage and conservation status in the Benguela Upwelling Ecosystem

Large populations of seabirds occur in the Benguela Upwelling Ecosystem, with 15 species of seabird and an endemic shorebird breeding within this system (Kemper *et al*. 2007) (Table 1). Ten of these species are endemic to southern Africa, two as subspecies, breeding on coastal islands and mainland sites within southern Africa. Of these 16

species, 11 have IUCN threat status assigned to them (Table 1). The species that has undergone the largest change in population status is the African penguin. In 2000 it was classified as 'Vulnerable,' but has since been reclassified as 'Endangered' in 2010 (BirdLife International 2010). This thesis focuses on the African penguin and issues relating to its conservation and management.

Seabirds as indicators

Most flying birds can be thought of living in two media, that of air and land. Marine birds however, switch between land, water and air, and often do so daily (Schreiber and Burger 2002). This flexibility has resulted in physiological and morphological adaptations to their environment, which has had an impact on their behaviour, ecology and demography (Schreiber and Burger 2002). Seabird life history traits are often referred to as extreme, with long life (20–30 years), deferred maturity (breeding can be delayed up until 10 years of age), small clutch size (often one egg), and extended chick rearing periods (sometimes up to six months) (Ashmole 1971, Schreiber and Burger 2002). About 95% of seabirds are colonial breeders, and become central place foragers (Orians and Pearson 1979) in breeding seasons in order to brood and feed chicks. Being highly adapted to the environment in which they live, they are sensitive to ecosystem changes (Croxall 1992), and thus seabirds are highly vulnerable to threats at and around their breeding colonies such as disturbance, pollution and over-fishing.

Since seabirds are near-apex predators, they have the potential to provide an index of the health of marine ecosystems (Underhill and Crawford 2005). They are ocean samplers, and can be used as indicators of location and variability of marine resources, including those exploited by commercial fisheries (Berruti *et al.* 1993, Cherel and Weimerskirch 1995, Weimerskirch *et al.* 2008, Mullers and Navarro 2010), and also of ecosystem changes and changes in rates of fished resources (Crawford *et al.* 2002, Boersma 2008). Pelagic fish are mobile, patchily distributed and are difficult and expensive to survey (Cherel and Weimerskirch 1995). Dietary data from top predators are relatively inexpensive to obtain, easily collected and are able to be collected at a more frequent and broader spatial scale that conventional oceanographic methods are not able to (Imber and Berruti 1981, Cherel and Weimerskirch 1995). Top predators can therefore provide information useful in the management of prey resources (BCLME Top Predators Project Steering Committee 2007).

The top predators project of the Benguela Current Large Marine Ecosystems (BCLME) project was funded through the Global Environment Facility, the objectives of which were to assess the utility of top predators as biological indicators of ecosystem change in the BCLME, and to implement an appropriate, integrated, system-wide monitoring programme to support the management of the BCLME (BCLME Top Predators Project Steering Committee 2007). Final recommendations with respect to seabirds included ensuring seabird monitoring programmes gained information on the following (not inclusive list) (Kemper 2007):

- the variability in seabird abundance, distribution and other biological parameters, such as breeding performance and body condition indices to assess population trends and conservation status of individual species as well as to assess the usefulness of using these parameters as indices of ecosystem health
- the diet, foraging behaviour and ecology of seabirds, particularly those feeding on commercially important prey species to gain information on the abundance and distribution of prey resources, to detect changes in the diet and in tropic flows and to establish food requirements of seabirds
- predator/prey and competition interaction effects on ecosystem structure and functioning and its effect on fisheries

It is within this context that this project was undertaken. It focuses on one seabird in the Benguela Upwelling Ecosystem, yet the issues covered have a broader application within this ecosystem. The discussion below details aspects of seabird biology and demography that can be used to provide information on the broader marine environment in general and for the African penguin in particular.

Prey: pelagic anchovy and sardine

Like other eastern boundary upwelling systems, the southern Benguela supports abundant populations of small pelagic fish such as anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax*. In the Benguela Upwelling Ecosystem, four species of seabird (African penguin, Cape cormorant *Phalacrocorax capensis*, Cape gannet *Morus capensis* and swift tern *Sterna bergii*) feed mainly on sardine and anchovy (Crawford and Dyer 1995).

Sardine was dominant in the northern Benguela from 1950 to 1975 and then collapsed in the mid-1970s as a result of purse-seine fishing (Crawford 2007). A slight recovery was observed in the 1990s, but a combination of an extreme low oxygen event in 1994

(Monteiro and van der Plas 2006), a warm water intrusion in 1995, together with fishing pressure on a series of poor recruit years, led to further declines in the biomass and catches (Boyer *et al*. 2001, Boyer and Hampton 2001). They have since remained at a low level (van der Lingen *et al*. 2006). In the southern Benguela, catches of sardine peaked during 1958–1962, and then catches declined to low biomass, as anchovy replaced sardine in the ecosystem (Hutchings *et al*. 2009a). From 1982/83, sardine biomass and catches increased until the early 2000s, when both sardine and anchovy peaked as a result of exceptional recruitment in consecutive years of 1999/2000–2002/03 (Hutchings *et al*. 2009a, DAFF unpubl. data). These exceptional recruitment years were followed by five successive years of poor recruitment, where sardine estimates declined sharply from over four million tons in 2002 to 260 000 tons in 2007 (Coetzee *et al*. 2008). This decline in sardine, led to an anchovy dominance in the system (Hutchings *et al*. 2009a).

These two fish species contribute the bulk of the catch of South Africa's purse-seine fleet (Crawford 2004) and are used to produce fish meal, oil (anchovy), human and pet food (sardine) (Hutchings *et al*. 2009a). Catches by the fishery have averaged close to 400 000 tonnes yr^{-1} over the past 50 years, and although the fishery initially targeted sardine, anchovy have dominated since the mid-1960s (Lehodey *et al*. 2006). Management of the South African pelagic fish stock is conducted through an operational management plan (OMP) which sets Total Allowable Catch (TAC) limits for directed and bycatch of sardine of approximately 12–14% of the total biomass estimated from the acoustic surveys (Hutchings *et al*. 2009a). The way in which these hydro-acoustic surveys are conducted is further discussed in Chapter 2.

Moult

Moult in birds is considered unexpectedly energetically expensive (Hoye and Buttemer in press). Moult in penguins is unique, since they replace all their feathers in a relatively short period of time compared to that of other birds, ranging from 13– 40 days depending on the species (Stonehouse 1967). Moult in penguins is an essential feature to them being able to remain waterproof and thus insulated in cold waters while foraging (Stonehouse 1967, Payne 1972). Penguins become hyperphagic during the pre-moult period (Otsuka *et al.* 2000), and the acquisition of sufficient body reserves during pre-moult foraging can be considered a greater priority than at any other time in the annual cycle (Croxall and Davis 1999, Wolfaardt *et al.* 2008,2009a). Penguins are thus dependant on high and predictable food availability during the pre-moult fattening and

post moult recovery phases. An understanding of timing of moult, including when and where pre-moult fattening and post moult recovery takes place is of critical importance for penguin conservation management.

Studies of moult patterns in terms of synchrony and seasonality have shown colony specific variability (Underhill and Crawford 1999, Crawford *et al.* 2006a, Kemper 2006,Wolfaardt *et al.* 2009a), which may be attributed to variation in available food resources around the colonies, providing further examples of use of seabirds as indicators. If a greater proportion of adults are moulting than breeding, it can be indicative of poor breeding conditions, or poor condition of breeding adults, since established breeders are abstaining from breeding (Crawford *et al.* 1999). Analysing moult and breeding trends per colony, can provide an indicator as to the trends of that specific population, local availability of food resources, as well as provide an indication site fidelity and movement of individuals between colonies during the various stages of the penguin annual cycle and the success of artificially raised and released chicks that are observed as moulting juveniles (Whittington *et al.* 2005a,b, Kemper *et al.* 2008, Wolfaardt *et al.* 2009a).

Condition

Reproductive performance of seabirds can be used as indicators of food availability (Cairns 1987, Williams and Croxall 1990, Boersma 2008). Since seabirds are central place foragers when breeding, returning frequently to their chicks to provision for them, studies of the growth and condition of chicks can be an indicator of feeding conditions around the breeding colony (Williams and Croxall 1990, Bradshaw *et al.* 2000). Sherley (2010) studied the growth rate of African penguin chicks at five African penguin colonies in South Africa, investigating the spatial and temporal variability between years and colonies. This thesis provides a complimentary study, using an index of chick condition that was developed using African penguin chicks from Robben Island (Lubbe 2008). The primary difference in using the condition index approach, is that it is able to make use of a random sample of unknown chicks, as compared to that of growth rate studies that follow the growth rate of individual chicks till fledging.

Foraging

Most species of seabirds spend a considerable proportion of their lives feeding at sea, often out of sight of land; this makes foraging behaviours difficult to study and understand, because observations are difficult to make (Schreiber and Burger 2002).

Their at sea activities usually consist of migration or foraging. Understanding their foraging ecology is of critical importance in their conservation (Frost *et al*. 1976).

Until near the end of the 20th century, attempts to locate seabird feeding areas and associated prey aggregations relied on visual observations, that more often than not relied on the availability of oceanographic cruises (Cherel *et al*. 1995). The development of satellite tracking for large seabirds (Jouventin and Weimerskirch 1990) enabled the development of a more thorough understanding of seabird foraging ecology and secondly to use these marine predators to provide insights into the location of their prey (Cherel *et al*. 1995). Satellite fixes have enabled the foraging journeys of foraging seabirds to be accurately mapped, allowing for the identification of feeding areas (Weimerskirch *et al*. 1993, Weimerskirch and Robertson 1994). Advances in the development of technology have resulted in our ability to learn more about the diving behaviour of foraging birds, with the development of miniaturised electronic time-depth recorders (TDRs) that allow detailed descriptions of at-sea behaviour (Wilson 1985). This provides an opportunity to investigate how different populations of the same species change their diving pattern according to different marine habitats (Tremblay and Cherel 2003). GPS-TD devices small enough to equip African penguins, became available in the early 2000s (Ryan *et al*. 2004, Petersen *et al*. 2006).

Seabirds have different foraging behaviours, and changes in food supply will affect species differently. A change or decreasing food supply will potentially, for example, impact the African penguin sooner and more intensely than a flying seabird due to its limited foraging range (Pichegru *et al*. 2009). Certainly it is the African penguin that has undergone the most recent rapid decline in the Benguela Upwelling Ecosystem compared to any other seabird species (Crawford *et al*. 2011), and the study of the African penguin foraging behaviour can provide clues as to the mechanisms behind these declines.

Legislation

One of the objectives of this thesis is to make the linkages between research and legislation. Here, the scope of this exercise is in the Benguela Upwelling Ecosystem, with an emphasis on the linkages between research and legislation for the study species of this thesis, the African penguin. An obvious example of this kind of linkage exists between the fisheries scientists whose responsibility it is to estimate fish stocks, and the legislation in terms of which fishing quotas are issued to fishers. The linkages between

seabird research and the legislation related to seabirds, mainly seabird conservation, is less direct, and this thesis explores aspects of this relationship.

Angola, Namibia and South Africa are the three countries responsible for the protection of species within the Benguela Upwelling Ecosystem (BCLME Top Predators Project Steering Committee 2007). In South Africa, the protection of seals and seabirds has been largely within the framework of the Seal and Seabirds Act (No. 46 of 1973). With increasing pressure on the marine environment and the top predators, specifically seals and seabirds, this act became outdated. Biodiversity conservation in South Africa has historically been fragmented and uncoordinated, largely focused within the different provinces (Smith 2005, Blackmore 2006). With the development of the National Environmental Management Act (No. 107 of 1998), a framework has been created to provide for biodiversity conservation of terrestrial and marine species, with a strong emphasis on the State trusteeship of protected areas, and responsibility for conserving biodiversity within the context of co-operative governance. Key principles in implementing this legislation, is public participation, and the reliance on science to guide decision making. This provides the platform for increased public and stakeholder engagement and accountability on the part of the State. Additionally, it facilitates scientists and NGOS that operate within the field of conservation, especially in endangered species, to engage with the relevant managing and regulatory authorities to ensure that their research agendas and activities support the conservation mandate and responsibility of the state.

The offshore islands in South Africa are managed by South African National Parks, CapeNature and Robben Island Museum. This thesis (Chapter 6) explores a mechanism through the biodiversity legislation by which all state, tertiary and NGOs are able to work together toward a unified African penguin management plan.

Study Site: Dyer Island

The Dyer Island complex, consisting of Dyer Island and Geyser Rock (34°41'S 19°25'E) (Figure 3), is one of 14 and the most southern of the offshore islands off the South African coastline. It is the easternmost of the chain of seabird islands of the Western Cape, and the link between islands in the Western and Eastern Cape. Dyer Island is considered by Birdlife South Africa to be one of 101 Important Bird Areas (IBAs) in South Africa (Barnes 1998).

Dyer Island is located approximately 12 km southeast of Danger Point and 9 km from Kleinbaai harbour (Barnes 1998). It is 20 ha, 900m at its longest axis, and 200m at its widest, with a perimeter of 2.4 km. The island is flat, low-lying and not more than 9 m.a.s.l. Geyser Island (approximately 2ha), is a Cape fur seal (*Arctocephalus pusillus pusillus*) breeding colony, with c. 11 000 pups recorded in 2004 (Kirkman *et al.* 2007). Geyser Island lies approximately 150 m to the southwest of Dyer Island (Figure 3). Shark Alley separates Dyer Island Geyser Island, making this an internationally recognised shark cage diving destination.

Dyer Island was named after the first resident of the island, Sampson Dyer, an American slave who arrived at Dyer Island in 1806, whose primary task was seal harvesting (Fourie 2002). Seal harvesting took place from the 17th to the 19th century along the southern African coastline (David and van Sittert 2008), undoubtedly causing disturbance to breeding birds on the island. In 1832 the guano deposits on the coastal islands around South Africa were discovered by an American sailor Benjamin Morrel, and in the mid 1800s, the British ships sailed to the southern African coastline to harvest this valuable source of fertilizer (Fourie 2002). In the 1700s, penguin eggs became a popular delicacy among the public (Frost *et al.* 1976), and penguin egg collection continued until the 1960s. Egg collection on Dyer Island occurred from 1875 till 1968, with the largest annual harvest recoded in 1905 when 62 500 eggs were collected (Shelton *et al.* 1984). Egg collection, guano harvesting as well as the associated disturbance would undoubtedly have had an impact on the number of birds that would have recruited into the breeding population (Shannon and Crawford 1999).

Under the authority of the Cape Provincial Administration, South Africa, all offshore islands were declared Provincial Nature Reserves in 1988 and were placed under the control of the then Department of Nature Conservation of the Cape Province. Dyer Island is currently (2010) managed by the Western Cape provincial conservation body, the Western Cape Nature Conservation Board (CapeNature).

Twelve species of seabirds (Table 1) and five terrestrial species breed on Dyer Island. In 1978, Dyer Island was considered to have the world's largest breeding population of African penguins of approximately 27 000 pairs and about 70 000 total penguins overall (Shelton *et al.* 1984, Crawford *et al.* 1995b). In 2010, the breeding population was < 2000 pairs (Crawford *et al.* 2011, Chapter 2, 3).

Study Species: African penguin

There are 18 species of penguin in the world, thirteen of which have a concerning IUCN conservation status (Table 2). Five species are considered Endangered, two of which are in the genera *Spheniscus*.

The genus Spheniscus

The African penguin is one of four species in the genus *Spheniscus*; three breed in South America, and this is the only penguin species to breed in Africa (Shelton *et al*. 1984). The Galapagos penguin *S. mendiculus*, is the northernmost of all penguins and is endemic to the Galapagos Islands, breeding on Fernandina and Isabela Islands on the equator (Boersma 1977, Vargus *et al*. 2005). The Magellanic penguin *S. magellanicus* breeds in Chile, Argentina and the Falkland Islands (Wilson *et al*. 1995) and the Humboldt penguin *S. humboldti* is endemic to the Humboldt Current, and breeds in Peru and Chile (Wilson *et al*. 1995). *Spheniscus* species are generally allopatric, although the ranges of the Humboldt and Magellanic penguins overlap in northern Chile (Wilson *et al*. 1995).

In terms of their movement and seasonal patterns in their life history, African penguins and Humboldt penguins have been recorded breeding throughout the year, and when not breeding tend to stay at their breeding colonies, although may travel long distances during the pre-moult fattening, and post-moult recovery periods (Culik and Lun-Jorquera 1997, Whittington *et al*. 2005a). Magellanic penguins are seasonal breeders and migrate away from their breeding colonies during the non breeding season (Boersma *et al*. 1990, Croxall and Davis 1999, Yorio *et al*. 2001). Galapagos penguins do disperse when not breeding, but have limited movements compared to the other *Spheniscus* species (Boersma 1977).

Population trends of the African penguin

The African penguin is endemic to the Benguela Upwelling Ecosystem (Frost *et al*. 1976, Shelton *et al*. 1984). This breeding range is split into three distinct regions, southern Namibia, the Western Cape and Eastern Cape of South Africa (Whittington *et al*. 2005a). African penguins breed at 25 islands and four mainland localities in Namibia and South Africa, indicating the significance of these offshore islands in southern Africa (Kemper *et al*. 2007). As penguin numbers declined through the 20th and 21st century, some sites previously occupied by penguins have become extinct, such as Seal Island, Penguin Island and Albatross Island in Namibia, and Bird Island, Lambert's Bay in South Africa

(Crawford *et al*. 1995a,b, Kemper *et al*. 2007). A colony at De Hoop in South Africa was established in 2003 and this was attributed to penguins attempting to bridge the gap between Dyer Island and the colonies in the Eastern Cape (Underhill *et al*. 2006).

The decline of the African penguin and concern for the future of the species were reported by Westphal and Rowan (1971). This was in the context of the first oil spills which resulted in large numbers of penguins being killed simultaneously. The magnitude of the decline however was unknown given that census data of all African penguin breeding colonies were unavailable. In 1910, it is estimated that were about 1.5–3 million individuals (Shannon and Crawford 1999). In 1956, this figure had declined substantially to approximately 0.3 million penguins (Rand 1963a,b). The next overall population assessment was conducted during the 1978/79 season when 70 000 breeding pairs were recorded, evidence of a further decline Shelton *et al*. (1984).

During the 1990s, further declines were again observed where 44 000 breeding pairs in 1993 were estimated (Crawford *et al*. 1995b). A recovery was observed in the late 1990s, early 2000s, where 63 000 pairs were counted in 2001 (Kemper *et al*. 2007). However, despite this promising increasing trend in the 1990s, the reverse has occurred in the 2000s. In South Africa, the number of breeding pairs collapsed from an estimated 56 000 breeding pairs in 2001, to 21 000 pairs in 2009, and the global population in 2009 was estimated at 26 000 (Crawford *et al*. 2011). It is the rapid decline from 2004 to 2009 that has led to the re-classification of the species from 'Vulnerable' to 'Endangered' (BirdLife International 2010).

Threats to the African penguin

Factors contributing to this decline in the early part of the 19th century included egg exploitation, habitat degradation and disturbance as a result of guano scraping (Frost *et al*. 1976, Shannon and Crawford 1999). Exploitation of penguin eggs began soon after the Dutch colonists settled in what was to become Cape Town. Although no records were kept of this initial exploitation, the penguin colony on Robben Island was extinct by 1800 suggesting this was substantial (Frost *et al*. 1976). Official records since 1881 showed over 13 million eggs were removed in the 30 year period 1900–1930 (Frost *et al*. 1976). The impact to the African penguin was substantially more, since partially incubated eggs were discarded, and well incubated eggs were deliberately destroyed to induce the penguins to relay to allow the collection of freshly laid eggs (Frost *et al*. 1976). Breeding birds were disturbed during this practise, causing nest desertion and predation on eggs

and chicks by kelp gulls *Larus dominicanus* (Frost *et al.* 1976). Guano harvesting removed breeding habitat, and caused further disturbance to breeding birds causing nest abandonment and kelp gull predation on eggs and small chicks. Although this practise has since ceased, the build-up of guano deposits has been prevented due to the low numbers of seabirds in the 21st century. African Penguins are not able to make burrows in the guano and so in most colonies, now breed on the surface, exposing the adults and chicks to heat stress, and eggs and small chicks to kelp gull predation. These two practises resulted in poor recruitment into the population in the 1900s (Shannon and Crawford 1999).

Wolfaardt *et al.* (2009b) provided a review of the impact that oiling has had on seabirds in South Africa, particularly African penguins and Cape gannets. Two of the most notable oil spills the *Apollo Sea* in 1994 and the *Treasure* in 2000 (Underhill *et al.* 1999, 2006, Crawford *et al.* 2000, Barham *et al.* 2007, Wolfaardt *et al.* 2009b). These two spills not only oiled estimated 10 000 and 19000 birds respectively, but Wolfaardt *et al.* (2008) reported on the lower breeding productivity of de-oiled African penguins. It is not only major spills that have an impact on this species. Chronic oiling through oil from leaking containers, or through the illegal practise of ships cleaning their bilges out at sea result in a number of penguins being oiled each year (Parsons and Underhill 2005). In 2005, c. 500 adult penguins were sent to SANCCOB due to chronic oiling, which represented about 10% of the total adult population at Dyer Island at that time (CapeNature unpubl. data).

Makhado (2009) documented the extent of Cape fur seal *Arctocephalus pusillus pusillus* predation on South African breeding seabirds, a source of seabird mortality on Dyer Island which is considered unsustainable. The great white shark *Carcharodon carcharias* is common in the waters surrounding Dyer Island is known to predate on African penguins Johnson *et al.* (2006). The number of kelp gulls on Dyer Island has increased steadily on Dyer Island since 1998 (Crawford *et al.* 2007), and are a source of predation pressure of African penguin eggs and small chicks on Dyer Island (LJW pers. obs.).

The greatest current threat to African penguins is considered to be the abundance and availability of prey (Crawford *et al.* 2007, Crawford *et al.* 2011). In the Benguela Upwelling Ecosystem, changes in the relative abundance of sardine and anchovy have been linked to changes in diet, breeding population size and breeding success of various

seabird populations, including Cape gannet, African penguin, Cape cormorant, and swift terns populations (Crawford and Dyer 1995, Crawford 2003, Crawford *et al*. 2006, 2007, Underhill *et al*. 2006). The reported eastward shift in the centre of gravity of purse-seine catches past Cape Agulhas of both sardines (Coetzee *et al*. 2008) and anchovy (Roy *et al*. 2007) is said to have creating a mismatch between fish availability and seabird breeding colonies during the summer spawning period, with significant implications for the seabirds of the region (Crawford *et al*. 2007).

Overview of this study

A recent shift in the southern African region towards an ecosystem approach to fisheries management (EAF) (Cochrane *et al*. 2009), embraces the concept of the use of the biological characteristics of top predators to monitor the state of prey resources or ecosystem changes, and provide information otherwise useful to the management of resources (BCLME Top Predators Steering Committee 2007). African penguins are considered top predators within the marine ecosystem (Wilson 1985), assimilating processes occurring at lower trophic levels and so can be considered good indicators of ecosystem changes (BCLME Top Predators Project Steering Committee 2007).

Given the rapid population decline since 2004 and subsequent 'Endangered' status; that African penguins are top predators and indicators of ecosystem changes and that lack of sufficient food resources are assumed to be responsible for the recent decline in numbers (Crawford *et al*. 2007); Marine and Coastal Management (MCM), the then sub-directorate of the Department of Environmental Affairs (DEA), initiated a two year pilot study to assess whether temporary fishing closures around offshore islands could have a positive impact on penguin breeding at these colonies (Crawford 2009a).

In the Western Cape, this resulted in a 10.8 nautical mile radius (20 km) area from the low water mark in the marine area around Dassen Island being closed to purse-seine fishing for two years from 15 January 2008–31 December 2009. In Algoa Bay in the Eastern Cape, a similar area around St Croix Island and a 5 km radius around the Riy Bank was closed for two years commencing 2009. Robben Island along the west coast, and Bird Island in the Eastern Cape, remained opened to fishing to serve as a control and duplicate monitoring was undertaken at all four islands. Results obtained from this study were used to assess the efficacy of using closed areas to improve the breeding success and survival rates of African penguins and to inform the design of possible future experimental closures (Crawford 2009a,b). Parameters that were used to monitor

the effects of these closures included: numbers of pairs breeding at colonies, numbers of birds in adult and immature plumage moulting, survival of adult birds, breeding success, chick condition, chick growth, foraging effort (including range, trip duration and diving behaviour) and diet of adults feeding chicks (Altwegg *et al*. 2009, Crawford 2009b).

Given the importance of the area around Dyer Island to the sardine fishery, and that there was no island to act as control, this island was not considered as part of the initial feasibility study. However, concerns were noted at the state of the African penguin population on Dyer Island, and at subsequent Island Closure Task Team meetings, the intention was stated to investigate potential measures at Dyer Island, once the initial two year feasibility study was complete. Duplicate monitoring was conducted on Dyer Island however, to form a basis for comparison for the other islands, as well as to provide a baseline level of monitoring prior to any further fishery management intervention.

Structure and outline of thesis

Each chapter of this thesis is written as an independent paper to facilitate the publication of results. Tables and figures are included at the end of each chapter, as are the references, which have resulted in some overlap in the introductory and referencing sections of each chapter.

Chapter 2 outlines the relationship between the estimates of spawners and recruits of anchovy and sardine, to the number of breeding and moulting penguins at seven African penguin breeding colonies within South Africa. It investigates whether there is spatial disparity of these relationships between colonies, and the implications of these relationships for the conservation of the African penguin at the different colonies.

Chapter 3 focuses on the moult phenology of adult plumaged African penguins and compares the pattern of moult in the Namibian and South African colonies.

Chapter 4 makes use of an index to assess spatial and temporal differences in chick condition at five South African colonies.

Chapter 5 analyses the foraging behaviour of breeding African penguins on Dyer Island

Chapter 6 summaries the legislative framework for biodiversity conservation in South Africa, and discusses how this can be used as an effective tool for the conservation of this species if effectively implemented.

Finally, in Chapter 7, I attempt to synthesise the findings of all the separate chapters to provide an overview of the work as a whole. Suggestions for future research are provided.

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Table 1: Breeding seabird species in the Benguela Upwelling Ecosystem, their conservation status, and breeding status on Dyer Island

Species		Endemicity	Conservation status assigned in 2007*	Breed on Dyer Island (2010): Y-yes, N-no
African penguin	*Spheniscus demersus*	Endemic to southern Africa	Endangered (global)**	Y
Leach's storm petrel	*Oceanodroma leucorhoa*	Widespread, isolated population in South Africa	Critically Endangered (southern Africa)	unconfirmed
Great white pelican	*Pelecanus onocrotalus*	Widespread (southern Africa)	Near-threatened (southern Africa)	N
Cape gannet	*Morus capensis*	Endemic to southern Africa	Vulnerable (global)	N
Cape cormorant	*Phalacrocorax capensis*	Endemic to southern Africa	Vulnerable (global)	Y
Bank cormorant	*Phalacrocorax neglectus*	Endemic to southern Africa	Endangered (global)	Y
Crowned cormorant	*Phalacrocorax coronatus*	Endemic to southern Africa	Least concern (global)	Y
White-breasted cormorant	*Phalacrocorax lucidus*	Endemic to sub-Saharan Africa	Least concern (southern Africa)	Y
African black oystercatcher	*Haematopus moquini*	Endemic to southern Africa	Least concern (global)	Y
Kelp gull	*Larus dominicanus*	Endemic as subspecies to southern Africa	Least concern (subspecies global)	Y
Hartlaub's gull	*Larus hartlaubii*	Endemic to southern Africa	Least concern (global)	Y
Greyheaded gull	*Larus cirrocephalus poicephalus*	Widespread	Least concern (subspecies global)	N
Caspian tern	*Sterna caspia*	Widespread	Near-threatened (southern Africa)	Y
Roseate tern	*Sterna dougalli*	Widespread, isolated population in South Africa	Vulnerable (southern Africa)	Y
Swift tern	*Sterna bergii bergii*	Endemic as subspecies to southern Africa	Least concern (subspecies global)	Y
Damara tern	*Sterna balaenarum*	Endemic to southern Africa	Near-threatened (global)	N

* Status assigned by Kemper *et al.* (2007)

** Status assigned by BirdLife International (2010)

Table 2: Global penguin species and their IUCN threat status (source: García Borboroglu PG, Boersma PD (in press)).

Species	IUCN Threat Status	Main Threats
Gentoo penguin *Pygoscelis papua*	Near Threatened	Disturbance by humans, local pollution, and potential interaction with fisheries
Chinstrap penguin *Pygoscelis antarctica*	Least Concern	Human disturbance (primarily tourist visitors), and interactions with fisheries
Adélie penguin *Pygoscelis adeliae*	Least Concern	Climate change, habitat degradation, human disturbance, oil pollution
King penguin *Aptenodytes patagonicus*	Least concern	Potential for competition with fisheries, and the increasing rain events at colony sites due to climate change
Emperor penguin Aptenodytes forsteri	Least Concern	Global warming, that can alter the sea ice extent and duration, as well prey distribution and abundance. Industrial fisheries on the crustacean and fish populations, habitat destruction, and disturbance at breeding colonies by the impact of tourism can also affect the Emperor penguin
Southern Rockhopper Penguin *Eudyptes chrysocome*	Vulnerable	Oceanographic changes caused by global warming, largely influencing food availability, commercial fishing, hydrocarbon exploration and exploitation and ecotourism
Northern Rockhopper Penguin *Eudyptes moseleyi*	Endangered	Climate variation, egg collection, competition and incidental capture in fisheries, habitat degradation
Fiordland Penguin *Eudyptes pachyrhynchus*	Vulnerable	Introduced terrestrial predators, human disturbance, commercial and recreational fisheries
Snares Penguin *Eudyptes robustus*	Vulnerable	Main conservation concerns are commercial fisheries, oceanographic changes, and oil spills
Macaroni penguin *Eudyptes chrysolophus*		
Erect-crested Penguin *Eudyptes sclateri*	Endangered	Vulnerable to local perturbations in the environment. Evidence suggests significant population declines in recent times. There are no threats identified for this species, due to their isolation from human activities
Royal penguin *Eudyptes schlegeli*		
Yellow-eyed Penguin *Megadyptes antipodes*	Endangered	Habitat destruction and fragmentation, disturbance, and introduced predators
Little (Australian) or Blue (New Zealand) penguin *Eudyptula minor*	Least Concern	Climate variation, presumed egg and chick collection, potential competition and incidental capture in fisheries, habitat degradation, introduced mammalian predators, oil pollution
Galápagos penguin *Spheniscus mendiculus*	Endangered	The increasing severity of El Niño cycles (believed to be caused by global warming) is the most serious threat to this species, because a particularly severe cycle could result in extinction of Galapagos penguins. Habitat degradation presumed egg and chick collection, potential competition and incidental mortality in fisheries, introduced mammalian predators, and oil pollution are other threats
African penguin *Spheniscus demersus*	Endangered	Oil pollution, fishery mismanagement, habitat degradation and food availability changes potentially linked to climate change

Magellanic penguin *Spheniscus magellanicus*	Near Threatened	Oil pollution by spills, fishery mismanagement, and food availability changes potentially linked to climate variability
Humboldt penguin *Spheniscus humboldti*	Vulnerable	Overfishing, and incidental mortality in fishing nets

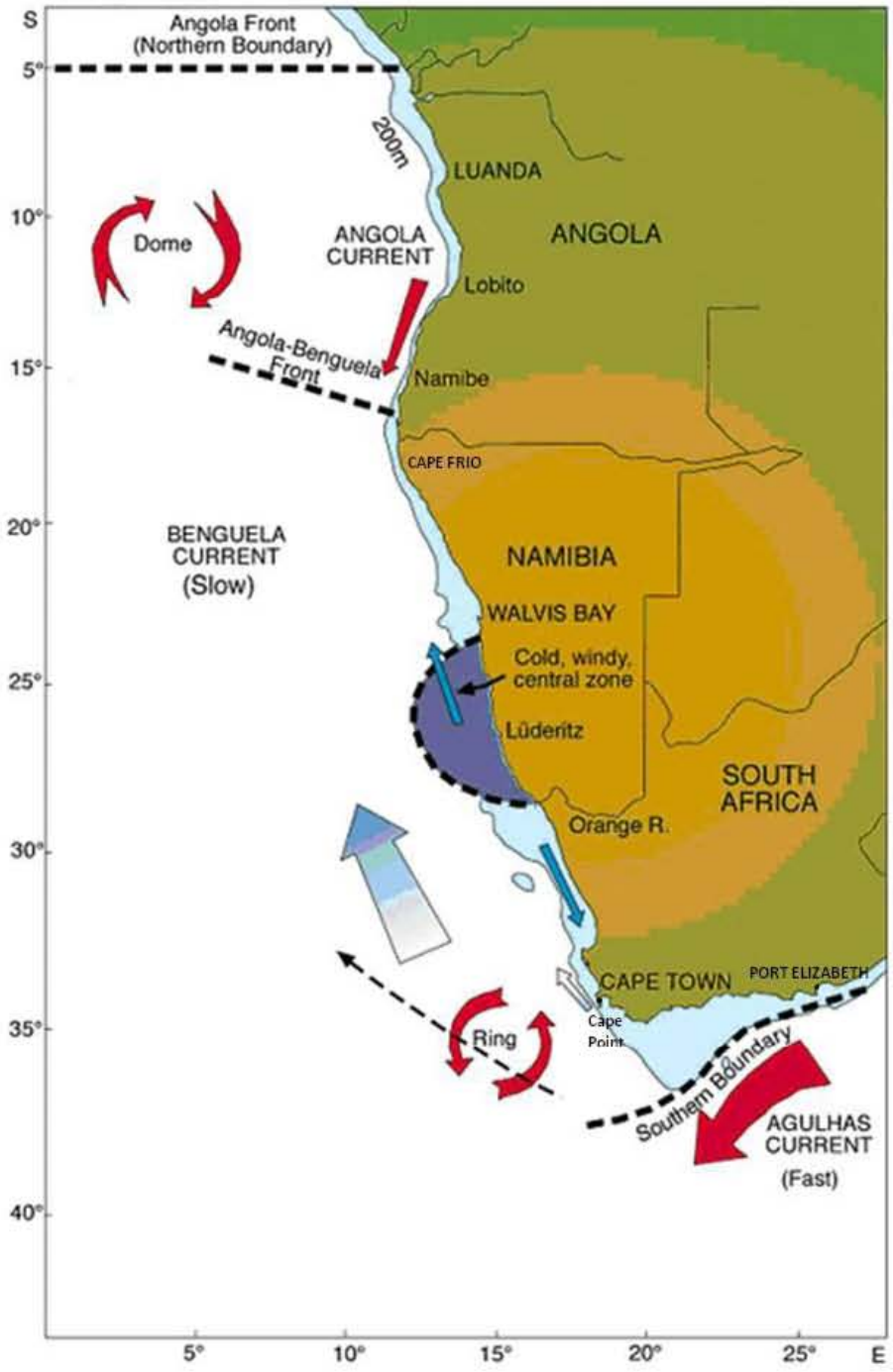

Figure 1: The Benguela Current Large Marine Ecosystem. (Map courtesy of Benguela Current Large Marine Ecosystem Programme

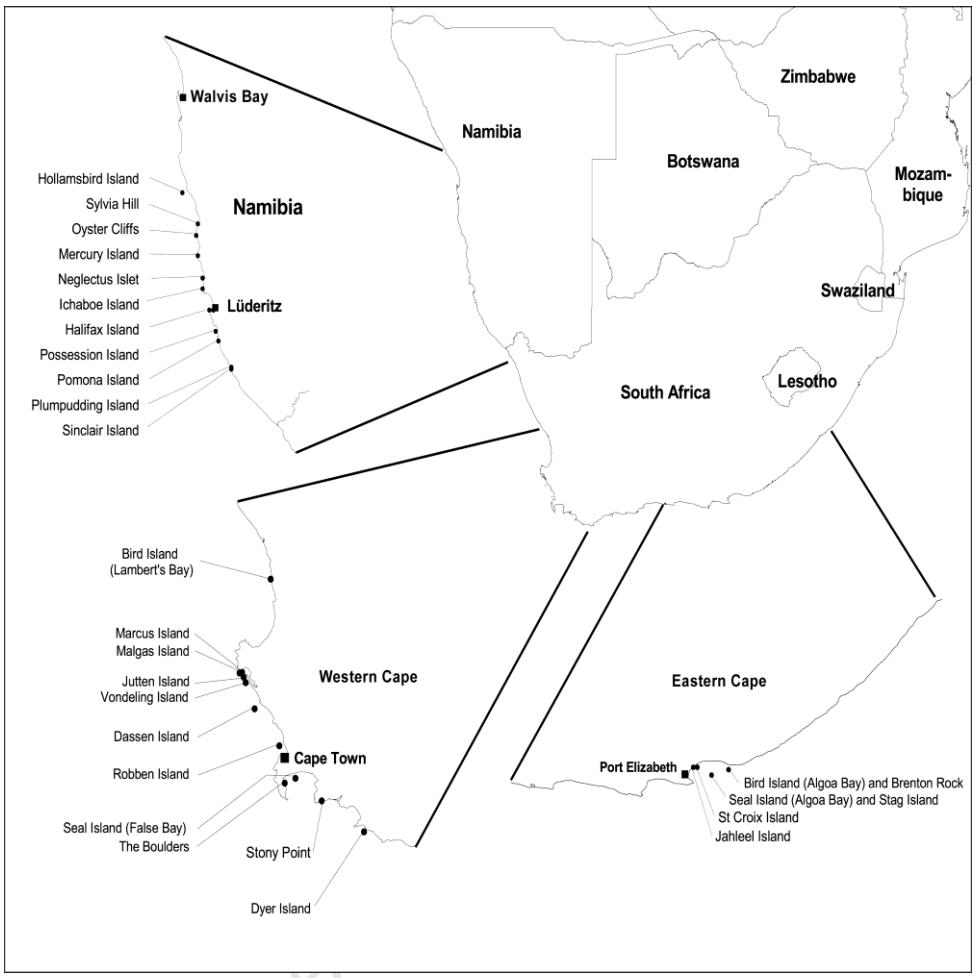

Figure 2: African penguin breeding localities in Namibia and South Africa. Map courtesy of Rene Navarro

Figure 3: Dyer Island on the west, and Geyser Rock on the east in this photo, separated by Shark Alley (c. 5m deep). Photo credit: R Jacobs

CHAPTER 2

RELATIONSHIPS BETWEEN AFRICAN PENGUIN COLONY SIZES AND BIOMASS OF PELAGIC FISH IN SOUTH AFRICA

Photo: L Waller

RELATIONSHIPS BETWEEN AFRICAN PENGUIN COLONY SIZES AND BIOMASS OF PELAGIC FISH IN SOUTH AFRICA

ABSTRACT

The relationship between African penguin *Spheniscus demersus* breeders and adult moulters to pelagic fish stocks was investigated at seven African penguin breeding colonies in South Africa. Spawner biomass surveys in November and recruit biomass surveys in May split the coastline into six and 10 strata respectively; biomasses of both Cape anchovy *Engraulis encrasicolis* and sardine *Sardinops sagax* were available for each stratum from both surveys for the period 1984 (spawner biomass) and 1985 (recruit biomass) to 2009. It was predicted that the strongest relationships would be found between number of adult moulters and the November spawner biomass of the previous year, within the stratum in which the colony was found, and that this relationship would be consistent across colonies. An unexpected relationship was found where adult moulters were correlated with spawner biomass of anchovy and sardine in the stratum south and east to that in which the Robben Island colony was found. The models relating breeders to pelagic fish stocks also demonstrated significant relationships with the November anchovy and sardine spawner biomass of the previous year. These correlational results suggest that the decision to breed for an African penguin might be largely determined by the condition which it is able to achieve prior to the moult fast of the previous year. Further research is needed in understanding the biological mechanisms of penguin-prey dynamics at a local, colony scale.

KEY WORDS

African penguin, anchovy, Benguela Upwelling Ecosystem, Bird Island, Dassen Island, Dyer Island, *Engraulis encrasicolus*, moult, recruitment, Robben Island, sardine, *Sardinops sagax*, spawner biomass, *Spheniscus demersus*, St Croix Island

INTRODUCTION

The African penguin *Spheniscus demersus,* a southern African endemic (Shelton *et al.* 1984, Kemper *et al.* 2001), has been in an overall population decline since early in the 20th century when there were an estimated 1.5–3.0 million individuals (Shannon and Crawford 1999). There were about 0.3 million penguins and 196 000 breeding pairs in

1956 (Rand 1963a,b). By 1978/79, the number of breeding pairs were estimated at 70 000 (Shelton *et al.* 1984). Further declines were observed up to 1993 (44 000 pairs), with a recovery observed in 2001 with 63 000 pairs recorded (Crawford *et al.* 1995a, Kemper *et al.* 2007). An accelerated decline from 2004 to 2009 resulted in the total global number of breeding pairs declining to 26 000 pairs in 2009, the lowest on record (Crawford *et al.* in press). This represented a decline of about 87% in the population in 53 years and has led to the reclassification of the species from "Vulnerable" IUCN to "Endangered" status in June 2010 (BirdLife International 2010).

The primary prey species of African penguins in South Africa are Cape anchovy *Engraulis encrasicolis* and South African sardine *Sardinops sagax* (Davies 1955, Rand 1960, Duffy *et al.* 1985, Wilson 1985a,b, Adams *et al.* 1992, Crawford and Dyer 1995, Crawford *et al.* 2006, in press). A number of studies have documented the relationship between African penguin population trends and food availability off Namibia, following the collapse of the sardine stock in the 1970s (Crawford 1998, Crawford *et al.* 2001), breeding African penguins in southern Namibia declined from 40 000 pairs in 1956 to about 1 000 pairs in 2000 (Crawford *et al.* 2001, Crawford 2007); the 96% decrease in breeding pairs at Possession Island between 1956 and 1995 was attributed to scarcity of food (Cordes *et al.* 1999).

Crawford (1998) related trends in regional populations of African penguins in South Africa to long-term changes in the abundance, distribution and availability of anchovy and sardine. Breeding success of African penguins in Saldanha Bay between 1984 and 1989, a period when sardine was increasing off South Africa (Barange *et al.* 1999), was positively related to the contribution of sardine to the diet (Adams *et al.* 1992). Reproductive performance of penguins at Robben Island is strongly influenced by the availability of food (Crawford *et al.* 1999). Between 1988 and 1993, the proportion of mature birds breeding on Robben Island was positively related to the spawner biomass of anchovy and from 1988 to 1995 to the spawner biomass of sardine (Crawford *et al.* 1999). Additionally, between 1989 and 1995 the mean number of chicks fledged per pair and immigration of immature birds were related to anchovy spawner biomass (Crawford *et al.* 1999). The growth of the colony at Boulders from 1985–1999 was related to abundance of anchovy (Crawford *et al.* 2000a). Crawford *et al.* (2008a) showed significant relationships between numbers of penguin breeding pairs in the Western Cape and recruitment biomass of anchovy and sardine, and spawning sardine biomass.

A positive correlation was found between the proportion of burrows occupied by breeding African penguin on Dassen Island from 1995 to 2008 and the overall biomass of sardine and anchovy (Durant *et al.* 2010).

This study investigates the relationships between African penguin population sizes and the biomass of anchovy and sardine measured on a smaller spatial scale than the earlier studies. The more detailed fish data are available for both the spawner biomass and recruit biomass surveys. There are two measures of the population sizes of African penguins: the breeding censuses yields the numbers of breeding pairs and adult moult counts provides an estimate of number of adult-plumaged penguins (Kemper 2007). Both measures were used in this study at seven penguin breeding colonies. The relationships between these two estimates of population size and the estimates of the biomass of sardine and anchovy within the same and adjacent strata to these colonies were investigated. The results are considered in terms of spatial management strategies required for the conservation of the African penguin.

MATERIALS AND METHODS

Fish data

Between 1984 and 2009, two hydro-acoustic surveys were conducted annually in South Africa: a survey in May to determine the distribution and estimate the biomass young-of-the-year (recruits) anchovy and sardine, and a survey in November with the same objectives for the spawner biomass (Hampton 1987, Coetzee *et al.* 2008a, DAFF unpublished data). These surveys were conducted by the Department of Agriculture, Forestry and Fisheries (at the time of the surveys reported, it was the Marine and Coastal Management Branch of the Department of Environmental Affairs and Tourism). The surveys covered the known areas of spawning and occurrence of young-of-the-year fish (Hampton 1987). The survey and sampling procedures were described by Hampton (1987) and Barange *et al.* (1999). The survey tracks were preselected, randomly-spaced, parallel transects, designed to obtain estimates of stock size with known precision (Jolly and Hampton 1990, Barange *et al.* 1999) (Figures 1 and 2). The strata were defined according to distribution patterns based on earlier experimental surveys in 1983 (Barange *et al.* 1999). Results for the November adult spawner biomass survey (Figure 3) and May juvenile recruitment biomass survey (Figure 4) were available from 1984 to 2009 (Janet Coetzee, Department of Agriculture, Forestry and Fisheries *in litt.*).

For these analyses, data were used from three strata of the November spawner biomass surveys (Stratum B: Cape Columbine–Cape Point, Stratum C: Cape Point–Cape Agulhas, and Stratum E: Mossel Bay–Port Alfred; Figure 1) and from three strata of the May recruitment surveys (Stratum D: Cape Columbine–Cape Point, Stratum E: Cape Point–Cape Agulhas, and Stratum I: Port Elizabeth–Port Alfred; Figure 2). The geographic limits of the strata were defined differently for the May and November surveys; for example, Stratum B in the May recruitment biomass survey is not the same area as that covered in Stratum B in the November spawner biomass survey. In this chapter, implicit to references to the November spawner biomass surveys are the strata used in that survey (Figure 1), and likewise the May recruitment survey uses the strata used in that survey (Figure 2).

Penguin data

This chapter considers data from seven breeding colonies in South Africa: Dassen Island, Robben Island, Boulders, Stony Point, Dyer Island, St Croix Island and Bird Island (Figures 1 and 2). Estimates of the numbers of African penguins breeding were obtained from annual counts of occupied nest sites conducted at these colonies during the main breeding season between 1979 and 2009 (Crawford *et al.* 1990, 1995a,b, 2001, Underhill *et al.* 2006, Chapter 3) (Table 1). Nest counts were usually conducted between May and June, the time of peak breeding for African penguins in South Africa (Randall 1983, Crawford *et al.* 1999), which coincides with the May recruitment biomass surveys. Crawford *et al.* (2006) excluded the year 2000 from their analyses of breeding success at Robben Island due to the oiling of breeders as a result of the sinking of the *Treasure* on 23 June (Crawford *et al.* 2000b) which led to an early termination of breeding. However, the penguin censuses for 2000 took place prior to the spill, which did not impact the standard way in which annual number of penguins breeding was measured.

Time series of at least 12 years of estimated numbers of African penguins moulting at each colony were available from three colonies in South Africa: Dassen Island, Robben Island and Dyer Island (Table 1). Counts were made of both immature and adult-plumaged birds; only the adult-plumaged penguins are considered in this chapter (Crawford *et al.* 1990, 1995a, Randall *et al.* 1986, Underhill and Crawford 1999, Kemper *et al.* 2008, Chapter 3). The available data were counts of moulting penguins around the coastline for Dassen Island and Robben Islands; as a result, an unknown, but presumably constant, proportion of penguins moulting in the interiors of the islands

were not included in the totals (Wolfaardt *et al.* 2009a,b, Underhill and Crawford 1999, Crawford *et al.* 2008a). The surveys conducted on Dyer Island included all moulting birds on the island (Chapter 3). Estimates of the annual numbers of adult-plumaged moulters were obtained using the method described by Underhill and Crawford (1999), Crawford *et al.* (2006), Kemper *et al.* (2008), Wolfaardt *et al.* (2009a,b) and Chapter 3. In South Africa, peak penguin moult is mostly in November (Chapter 3), coinciding with the November spawner biomass survey.

Data analysis

The general linear model was used to analyse the relationship between numbers of African penguin and fish biomass at colonies in the Western Cape and Eastern Cape. The objective of the analysis was to relate the numbers of breeding adults and the number of adult-plumaged moulters to the available sardine and anchovy adult biomass and juvenile recruitment within, and adjacent to, the stratum in which each colony is situated.

Explanatory variables used in the regression models were given a standard set of mnemonic abbreviations; for example, S is used to denote sardine and A anchovy (Table 2). For analyses investigating fish biomass in relation to the number of adult breeders, the models were restricted to the spawner biomass lagged by one or two years, given that the surveys were conducted in November, and the birds commence breeding mainly from March of the following year. Recruit biomass was not lagged, because the surveys were conducted in May, during the African penguin breeding season and were thus considered immediately available to breeding penguins.

Previous analyses that made use of the pelagic data focused on the spawner biomass and recruitment abundance of sardine and anchovy, sometimes simply added together. These fish species do not have the equivalent energetic values and it is useful to consider this in the analysis. I transformed the biomass of fish to kilojoules according the relationships 1g of sardine is 8.59kJ and 1g of anchovy is 6.74kJ (Batchelor and Ross 1984), so that anchovy has c. 80% of the energetic value of sardine. These are acknowledged to be average values, and vary seasonally (Schulein *et al.* 1995).

I listed plausible models that relate breeding numbers to explanatory variables for the data that were available. The terms were fitted and the model selection was guided by

both significance tests and the Akaike Information Criteria (AIC) (Akaike 1974). Models having smaller AIC values are preferred. Model fitting was done using GENSTAT 8.1 (Payne *et al*. 2010) within the framework of the general linear model.

For analysing time series data, the Box-Jenkins approach is acknowledged to be an appropriate statistical method (Box and Jenkins 1970). However, the time series in these analyses were too short to apply this method.

This is a desk-top statistical analysis exploring relationships between variables. The results obtained here cannot be construed as determining cause and effect. But the models revealed by this study suggest avenues of field research required to discover and confirm the mechanisms underpinning the relationships.

RESULTS

Breeding adults

Dassen Island

Several models for the number of breeding adults on Dassen Island over 16 years within the period 1984–2009 had similar AIC values (Table 3). The model with the smallest AIC contained two explanatory variables which both expressed food availability of sardine and anchovy in energy terms: kJ of sardine and anchovy in Stratum B in the two previous years (Table 3):

$$Br\_Das_i = 14157 + 2.418 \times Sp\_B\_AS\_kJ_{i-1} + 1.499 \times Sp\_B\_AS\_kJ_{i-2}$$

where Br_Das_i was the number of breeding adult penguins on Dassen Island at the time of the census in year i (usually April), and $Sp\_B\_AS\_kJ_{i-1}$ and $Sp\_B\_AS\_kJ_{i-2}$ were the combined energy values (expressed as MJ) of anchovy and sardine in Stratum B in the spawner biomass survey of the previous November and in the year previous to that (Table 2 gives the mnemonic conventions for naming variables). This model accounted for 54% of the variability in number of breeding adults. The model that simply combined the biomasses of anchovy and sardine provided a poorer fit (51%).

The best model with one explanatory variable for Br_Das_i contained the amount of anchovy and sardine, expressed in energetic value, in Stratum B during the previous

November's spawner biomass survey. Good models which contained spawner biomass in Stratum C, specifically that with sardine, were also obtained (Table 3). The relationship of African penguin breeders on Dassen Island to Stratum B, C and combined B and C of the combined November spawner biomass of anchovy and sardine are graphically displayed in Figure 5. No models with recruitment biomass in Stratum B and/or C were shown to have a significant relationship to Dassen Island breeders.

Robben Island

Several models for the number of breeding adults on Robben Island had similar AIC values. The model with the smallest AIC value contained two explanatory variables, both expressing food availability in energy terms in Stratum C in the previous two years. This model ran counter to my expectations, because Robben Island lies in Stratum B, and Stratum C lies to the south and east of it, from Cape Point to Cape Agulhas (Figure 1). This model accounted for 61% of the variability in numbers of Robben Island breeders (Table 4):

$$Br\_Rob_i = 1232 + 0.365 \times Sp\_C\_AS\_kJ_{i-1} + 0.338 \times Sp\_C\_AS\_kJ_{i-2}$$

where Br_Rob_i is the number of breeding adult penguins on Robben Island in year i, and $Sp\_C\_AS\_kJ_{i-1}$ and $Sp\_C\_AS\_kJ_{i-2}$ are the combined energy values (MJ) of anchovy and sardine in Stratum C in the spawner biomass survey of the previous November and in the year previous to that.

No models with (November) Stratum B spawner biomass or (May) Stratum D recruits were shown to have a significant relationship to Robben Island breeders, although these are the strata within which Robben Island falls for these surveys (Figure 1). While spawner biomass (November) in Stratum B was not significantly related to Robben Island breeders and that in Stratum C (November) was, the combined Western Cape (Stratum B&C) spawner biomass of anchovy and sardine expressed in energy terms was the model which explained the largest variability (51%) for a single term model (Table 4). The relationship of African penguin breeders on Robben Island to Stratum B, C and combined B and C of the combined November spawner biomass of anchovy and sardine are graphically displayed in Figure 6.

Other Western Cape Colonies

The number of breeding adults at Boulders were related to spawner biomass of anchovy and sardine of the previous year in Stratum C, the stratum in which it is located (r^2=24.1%, df=16, $p<0.05$) (Table 5). Boulders breeding adult penguins were also related to the biomass of anchovy alone for the same and for the previous year (Table 5). Western Cape spawner biomass of the previous year was correlated with the number of Boulders breeding adults, (r^2=18.3%, df=15, $p<0.05$) (Table 5).

While no relationships were found with recruitment biomass in the stratum in which Boulders is located (Stratum D), a significant relationship was found with kilojoules of recruitment in the adjacent stratum (r^2=30.5%, df=15, $p<0.05$) and combining the kilojoules of recruits in Stratum D and E gave a strong relationship Boulders breeders (r^2=24.7%, df=16, $p<0.05$) (Table 5).

At Stony Point the model combining the kilojoules of adult anchovy and sardine (November) in Stratum C of the previous year and kilojoules of recruitment in (May) Stratum E of the same year had the strongest relationship to Stony Point breeders, although only explaining 17% of the variance (Table 6).

The best relationships found for Dyer Island breeders was with the kilojoules of anchovy and sardine recruits in Stratum E (r^2=13.6%, df=14, $p<0.05$), and in Stratum E and D combined (r^2=13.6%, df=14, $p<0.05$), both of which had the same AIC value (Table 7). No relationship was found with November biomass in Stratum C and Dyer Island breeders for the variables available, or for the combined anchovy and sardine November biomass for the Western Cape of the previous year. The relationship of African penguin breeders on Dyer Island to Stratum B, C and combined B and C of the combined November spawner biomass of anchovy and sardine are displayed in Figure 7.

Eastern Cape

At St Croix, no significant relationships were found for breeders and fish parameters (Table 8). Biomass (r^2=16.2%, df=13, $p=<0.05$) and kilojoule models (r^2=16.2%, df=12, $p=<0.05$) of anchovy in Stratum E accounted for the greatest variability in Bird Island breeding adults (Table 9).

Overall relationships for Western Cape and Eastern Cape

Kilojoules of sardine and anchovy in Stratum C and B lagged by one year was the best fitting model for all colonies in the Western Cape combined (r^2=39.8%, df=16, $p<0.01$) (Table 10). The total number of penguins breeding in the Eastern Cape showed no significant relationships with any of the fish variables for Stratum E (November) or Stratum I (May) (Table 11).

Moulting adults

Plausible models between the estimated numbers of moulting adults at Dassen Island, Robben Island and Dyer Island and the fish variables were fitted (Table 12). At Dassen Island, the numbers of adult moulters were related to spawner biomass of sardine and anchovy in Stratum B of the previous year (r^2=32.4%, df= 12, p=0.01), as well as in the same year as the moult cycle begins (r^2=24.5%, df=12, $p<0.05$) (Table 12). At Robben Island, the number of adult moulters was related to the lagged sardine and anchovy adult biomass at Robben Island for stratum B (r^2=20.5%, df=16, $p<0.05$) (Table 12). The strongest relationship however was a model of the energetic value of sardine and anchovy and lagged by one year in stratum C (r^2=52.4%, df=16, $p<0.001$). The model was not improved when fish stratum B was included (Table 12). No correlations were observed between Dyer Island adult moulters and fish biomass estimates (Table 12).

DISCUSSION

The number of African penguins breeding at a colony is governed by four factors: (a) the number of breeders surviving from the previous year (and breeders have high fidelity to colonies), including a successful completion of moult; (b) recruitment to the breeding population, which is dependent on immature survival that could be influenced by conditions farther from the colony; (c) the decision to participate in breeding and good breeding success, which is reliant on adequate breeding condition (Crawford *et al*. 2008c) and (d) emigration/immigration of first breeders (Crawford 1998, Crawford *et al*. 2001). For (a) and (b), the food can potentially be some distance from the breeding colony (Barham *et al*. 2006); for (c) and (d) for African penguins, an adequate supply of food is needed close to the colony (Crawford *et al*. 2006, Wolfaardt *et al*. 2009b), and food must be available within c. 20–40 km of the colony (Petersen *et al*. 2006, Ludynia 2007, Pichegru *et al*. 2010, Chapter 5).

Wolfaardt *et al.* (2009b) hypothesized that the key component of the annual cycle of the African penguin was moult rather than breeding. One way to assess this idea is to compare the relative energetic costs of breeding and moulting. I therefore made approximate estimates of the energetic demands of both stages above the normal energy requirements. During breeding, the major additional energetic requirement is the provision of food for growing chicks. Bouwhuis *et al.* (2007) estimated the total energy intake for one chick over an average 68-day period from hatching to fledging to be 116.5 MJ, or an average of 1.71 MJ/day; the peak value was 2.35 MJ/day. Prior to moult, a penguin needs to increase in mass by c. 31% over c. 35 days. The average mass of an adult penguin is 3.14 kg prior to moult; the average increase in mass is thus 972 g. Using an estimated 30 kJ/g for these reserves (Klaassen 1996) and an assimilation efficiency of 0.76, the additional energy requirements of getting ready to moult are 38.4 MJ. Assuming that the energetic costs of biosynthesis are 0.33, as assumed by Bouwhuis *et al.* (2007) for chicks, the energetic costs of getting ready to moult are 51.1 MJ or an average of 1.50 MJ/day for the pre-moult period, similar to the daily energy demands of a chick during the pre-fledging period.

Mass loss during moult averages 47%, so the mass to be regained is c. 955 g over c. 42 days. Assuming mass to be regained is mainly protein, 6 kJ/g (Klaassen 1996), and allowing for the costs of biosynthesis, the energy requirements for recovery from moult are 7.5 MJ, but the process is probably physiologically extremely demanding, because it involves the recovery from a fast that has lasted at least 21 days (Randall and Randall 1986, Underhill and Crawford 1999, Kemper *et al.* 2008, Wolfaardt *et al.* 2009b).

There are other factors that also influence energetic requirements during the breeding season and the premoult period. For example, because penguins are central place foragers when they have nests (Wilson 1995, Petersen *et al.* 2006, Crawford *et al.* 2008b, Pichegru *et al.* 2010), daily commuting distances are longer during breeding than in the premoult period, when they do not have to return to the breeding colony. This would increase energy demand during the breeding period. On the other hand, during the premoult period body mass is gained, so there would be two ways in which energy demand would increase: the basal metabolic rate would grow as body mass increases, and the energetic costs of swimming and foraging with a heavier body would be elevated. The purpose of these calculations is to indicate the daily energy demands during breeding and moult might prove to be comparable. This supports the hypothesis of

Wolfaardt *et al.* (2009b) of the relative importance of moult in the annual cycle of the African penguin.

The primary prey of the African penguin, anchovy and sardine also form the bulk of the catch of South Africa's purse-seine fleet (Crawford 1980, 2004, Lehodey *et al.* 2006). In light of the decline in seabird numbers within the Benguela Upwelling Ecosystem (Kemper *et al.* 2007), and their dependency on pelagic prey, a series of correlational studies has discussed the impact of the commercial fishing industry in depleting prey availability for marine top predators such as the penguin, and the role that fisheries management should play in providing for efficient food resources for South Africa's declining sea bird populations (Okes *et al.* 2009, Pichegru *et al.* 2009, Durant *et al.* 2010, Crawford *et al.* in press). This paper continues this debate by relating annual measures of population size at the colony level to the estimates of prey availability in the same and adjacent strata in which the colony occurs.

Annual cycles of African penguins, sardines and anchovy

In the southern Benguela, the overall pattern of the annual cycle of the African penguin consists of preparation for moult in September/October, moult in November/December, post moult conditioning in December/January, and an extended breeding season from February to September, where the timing of breeding differs from colony to colony and is thought to coincide with local food availability (Crawford 1995a, b, Crawford *et al.* 1999, Wolfaardt *et al.* 2009b).

Sardine and anchovy in the southern Benguela have developed a reproductive strategy that is linked to the seasonal dynamics of the major environmental processes (Lehodey *et al.* 2006). This strategy is one of a spatial separation between spawning and nursery grounds. A simplified model for annual cycle of both anchovy and sardine is summarised into four components. Spawning of anchovy generally takes place on the Agulhas Bank (Figure 8) from August to February (Hampton 1987), peaking in November, at the same time as the spawner biomass survey (Hutchings *et al.* 1998). Sardine spawns year round with peaks in September/October and February/March (van der Lingen and Huggett 2003).

The ichthyoplankton of both species are transported by a northwest-flowing coastal jet current. This coastal jet acts as a 'conveyer belt,' transporting eggs and larvae from the

spawning area to the nursery grounds off the west coast in South Africa, from Cape Point towards the Orange River mouth (Lehodey *et al.* 2006). Initially the larvae are transported in currents, but once they are able to swim satisfactorily, they form shoals. The shoals of sardine and anchovy are initially mixed but as the fish get larger the shoals separate, and the shoals appear to move southwards in pulses (Armstrong and Thomas 1989). This migration of the juvenile fish occurs from about March of the year following spawning; the recruits (or young-of-the-year) migrate southwards along the west coast of South Africa to join spawning shoals of mature fish over the Agulhas Bank (Crawford 1980, Hutchings *et al.* 1998, Barange *et al.* 1999).

This migration occurs within c. 40 km of the coast so that juvenile fish are available to the breeding adults on the offshore coastal islands. This southward movement of recruits peaks in about May (and thus the May survey measures the recruits, and is closely timed to the penguin census) and continues until about September. The sardine recruits migrate southwards to merge with the adult sardines and anchovy recruits and become the spawning adults, both species returning to the Agulhas Bank and remaining there. The anchovy fishery is thus directed on the west coast, mainly at the recruits, i.e. first-year fish (Crawford 1980).

The distance between the Agulhas Bank and the larval entry point off the Orange River mouth where the southward migration commences is about c. 400 km. Assuming that recruits take six months to cover this distance, they would need to average c. 2 km/day. Assuming the radius of the feeding area accessible to penguins at a colony is c. 20 km (Petersen *et al.* 2006, Ludynia 2007, Pichegru *et al.* 2010), the diameter is 40 km, and a shoal of fish would therefore be available to breeding penguins for an estimated 20 days.

Based on the above annual cycles, my initial hypothesis was that the number of breeders at a colony in a year would be related to the November biomass of the previous year because sufficient food resources and thus good condition prior to the onset of breeding would be required for the decision to breed. Additionally, one could hypothesise that the number of breeders at each colony should be related to the biomass of recruits in May of the same year because they would need sufficient food in the vicinity of breeding localities to be able to provide food for their chicks. All previous work on African penguins shows that adults are range-restricted when breeding and so would be limited to foraging within a c. 20 km radius of the colony (Petersen *et al.* 2006, Pichegru et al.

2010, Ludynia 2007). I therefore hypothesised that this relationship would be strongest within the stratum in which the colony occurs.

Relationships between number of adult penguins and spawner biomass

Crawford *et al.* (2008a, Table 3) noted a positive relationship between the number of penguins breeding in the Western Cape and at Robben Island and recruitment biomass (sardines, anchovy and combined sardine and anchovy) one year earlier, and weak relationships between penguin numbers and the spawner biomass values half a year earlier. My results (Table 3–7), which were based on the decomposition of recruitment and spawner biomass into strata, showed a different, and more biologically meaningful, pattern than those obtained by Crawford *et al.* (2008a).

In this study, the number of breeders at Dassen Island was strongly related to the combined anchovy and sardine November spawner biomass of the previous two years within the stratum in which the island is located. At Robben Island, the number of breeders was similarly related to the combined anchovy and sardine November spawner biomass of the previous two years, but in this case, the relationship was with the stratum to the south and east of the one in which the island is located. A similar relationship was found in the models using the adult moult parameters. This suggests that feeding conditions between breeding seasons are somehow related to body condition at the onset of the breeding season and influence the penguin's decision to breed in the next breeding season, impacting on breeding numbers (Chastel *et al.* 1995, Gauthier-Clere *et al.* 2001, Crawford *et al*. 2008c).

In earlier studies, trends in regional populations of the African penguin have been related to overall food conditions with long-term changes on the abundance and distribution of sardine and anchovy assumed to be affecting breeding colonies in the same way (Crawford *et al.* 1990, 1995b, 2001, 2006, Crawford 1998, Underhill *et al.* 2006). It was thus unexpected that the relationships between numbers of breeders at Dassen Island and Robben Island and spawner biomass would be strongest in different strata, especially given that the two islands are only c. 50 km apart. At Boulders (c. 100 km from Robben Island), located near the eastern limit of Stratum C, the strongest relationships were found with spawner biomass of Stratum C. These correlational studies suggested that Dassen Island penguins prepare for moult in Stratum B, the stratum in which the island is located, whereas penguins breeding at Robben Island and

Boulders prepare for moult in Stratum C, the offshore area between Cape Point and Cape Agulhas (Figure 1). This is perhaps not totally unexpected, because the founder populations of both the Robben Island and Boulders colonies, are thought to have originated on Dyer Island, and much of the growth of these colonies in their early years is believed to have been fuelled by immigrants from Dyer Island (Crawford *et al.* 2000a). The penguins might therefore be returning to their "traditional" pre-moult fattening area, Stratum C. Additionally, during the non-breeding season (comprising the pre-moult fattening and post-moult fattening), African penguins are able to forage farther from their breeding colonies because they are not bound to having to return to feed chicks or relieve their incubating/guarding mate (Barham *et al.* 2006, Crawford *et al*. in press). An adequate supply of fish during this non breeding season is obligatory for them to gain sufficient reserves to have a successful moult, and to regain condition for breeding. These results suggest that food availability around the African penguin colonies is not uniform during the pre-moult fattening, and the post-moult recovery stages. If this is indeed the case, then the use of Robben Island and Dassen Island as "controls" for each other, for example in the "closures" project (Crawford 2009), is likely to be unjustified.

The penguin colony at Stony Point, founded at approximately the same time as the Boulders colony and the re-establishment of the colony at Robben Island, is also believed to have been founded and sustained by emigrants from Robben Island (Whittington *et al.* 2005). Unfortunately, standard protocol moult counts (Chapter 3) for the Stony Point colony are available only for 2000, 2009 and 2010. The numbers of penguins that moult at this colony are substantially larger than expected, given the number of breeding birds. The ratios of moulters in the moult season immediately following the breeding season were 21.9, 4.5 and 4.7 for the three years (Chapter 3, Table 5). In contrast, the number of penguins moulting on Robben Island was, between 2004 and 2009, less than the number of birds breeding (Chapter 3). The most parsimonious explanation of this anomaly is that some penguins that bred on Robben Island, prepared for moult in Stratum C, and then did not return to Robben Island to moult, but moulted at Stony Point. There are clear energetic benefits for this strategy, because it saves the costs of travelling c. 100 km while in a condition when travelling costs are maximal, with a full load of reserves.

The models for the number of breeders on Dyer Island showed no relationships to the November spawner biomass. This result was unexpected. Adult sardine concentrate on the western Agulhas Bank to spawn (Hampton 1992, van der Lingen and Huggett 2003). Furthermore, the area west of Cape Agulhas, incorporating the west coast, the southwest coast and the western Agulhas Bank, contained the bulk of the sardine biomass during the 1980s and early 1990s (Barange *et al.* 1999; Coetzee *et al.* 2008b). This spawning area is readily accessible to Dyer Island penguins. Thus, while the biomass was reportedly high in the area close to Dyer Island, the African penguin population collapsed (Crawford 1999, Crawford *et al.* in press). As found in the spawner models, no relationships between Dyer Island moulters and fish models were found. This suggests that factors other than the biomass of fish impacted the number of African penguins breeding and moulting on Dyer Island. The most likely factor is unsustainable levels of predation by Cape fur seals *Arctocephalus pusillus pusillus* (Marks *et al.* 1997, Makhado 2009, Crawford *et al.* in press, CapeNature unpubl. data). I suggest that that seal predation was a factor preventing an increase in the penguin breeding population on Dyer Island, inhibiting it from responding positively to the eastward displacement of prey resources.

In addition to the threat from seal predation, the impact, if any, of the sardine fishery concentrated around Dyer Island, needs to be investigated further. Crawford *et al.* (1995b) attributed the decline in the breeding population at Dyer Island from 22 655 pairs in 1979 (Shelton *et al.* 1984) to between 2000 and 3000 pairs from 1997–1999 to a reduced availability of anchovy to birds as indicated by the low anchovy biomass recorded in the hydro-acoustic surveys.

At Bird Island, a positive relationship was found with the biomass of anchovy in November in the stratum in which the island is located and breeding adults of the same year, but no relationship was found at St Croix Island. The area covered in Stratum E during the November survey is possibly too large compared to that of the foraging range of breeding penguins for a biologically meaningful result to be determined, and fish surveys subdividing Stratum E would be useful in exploring these relationships.

Relationships between number of adult penguins and recruit biomass

African penguin chicks on Dassen Island and Robben Island are fed primarily on first-year anchovies caught by the adults as they migrate past the islands from nursery

grounds located to the north (Crawford *et al.* 2006). Crawford *et al.* (2008a) found a positive relationship with the number of penguins breeding in the Western Cape to total combined recruit biomass of anchovy and combined anchovy and sardine biomass both of the previous year. Positive relationships were also found with breeders at Robben Island and total anchovy recruits, total sardine recruits and total anchovy and sardine recruits combined, all of the previous year (Crawford *et al.* 2008a). In this study, the result of no relationship of penguin numbers to recruit biomass at Dassen Island and Robben Island is perhaps not surprising. Since the May survey is conducted at a time when the penguins have already started to breed, the May recruit survey would not have an impact on the numbers of penguins breeding. However, an adequate supply of food resources around the breeding colony must be available in order for the successful fledging of chicks (Crawford *et al.* 2008b). Chick growth and chick condition as well as breeding success would be parameters more likely to be related to the May recruitment survey.

Overall Comments

A number of studies on the diet of the African penguin have confirmed the dominance of the pelagic anchovy and sardine (Rand 1960, Randall and Randall 1986, Wilson 1985a,b, Crawford *et al.* in press) highlighting the selectivity of the African penguin for these species, and ultimately their dependence on these fish species for their survival. Crawford (2004) identified the importance of ensuring adequate food availability around breeding colonies, as a key factor for the conservation of the African penguin. It is not only fish availability during the breeding season that is important. This study shows that the availability of food during the African penguin moult period is of critical importance to its survival.

Additionally, the dynamics of the relationship of penguins at the different African penguin breeding colonies to the surrounding fish biomass is not uniform. The difficulty with interpreting these relationships, is that the fish and penguin data sets are assimilated at different temporal and spatial scales, making it difficult for interactions to be detected, and if they are, to assess whether these interactions are biological meaningful. There is also substantial variability in the estimates of stock for each year and in each stratum each year. The abundance and distribution of anchovy and sardine has been shown to fluctuate widely (Hutchings *et al.* 2009), the transport of eggs and larvae itself has a strong seasonal signal, highly dependent on the location of local

spawning (van der Lingen and Huggett 2003). Decadal regime shifts in the distribution and abundance of these fish species do occur (van der Lingen *et al.* 2006). All these factors highlight the variability of this system, making it difficult to determine cause and effect relationships. The hydro-acoustic surveys provide a snap-shot of a mobile pelagic fish biomass and the likelihood of an over- or under-estimate of overall, year-round fish stock biomass is a possibility.

That the penguin population estimates are shown to respond differently at different islands suggests that there may be differences in local fish availability at a colony scale. Studies on anchovy reproductive ecology revealed a significant eastward shift of the anchovy spawning grounds after 1995 (van der Lingen *et al.* 2002, Fairweather *et al.* 2006). This has resulted in a spatial mismatch between penguin breeding localities and their food, especially along the west coast (Crawford *et al.* 2008a). Despite shifts in distribution of these stocks, large catches of anchovy and sardine were sanctioned, but not spatially managed, which may have led to the rapid decline of penguins along the west coast (Wolfaardt *et al.* 2009b, Crawford *et al.* 2011). However, results in this study show that the colonies such as Dyer Island in the south, and St Croix and Bird Islands in the Eastern Cape did not respond to this eastward shift as one might expect.

Smaller scale fish surveys at a colony level which would attempt to quantify the spatial and temporal patterns of fish availability at a colony level would greatly assist in our understanding of penguin-prey dynamics. These surveys are expensive and logistically time consuming and so the continuation of existing time series on marine top predators that utilise these pelagic fish stocks such as the African penguin is important. One of the shortcomings of this analysis was the lack of a time series of standard protocol African penguin moult counts at Stony Point and Boulders. The use of top predator parameters during the breeding season such as chick condition (Chapter 4) and breeding adult foraging behaviour (Chapter 5) are additional useful indicators to local fish availability. Additionally, there is a need for further information on the non-breeding season which includes diet, foraging areas, body condition, migration patterns, moult as well as adult condition and its implication for adult participation in breeding and breeding success.

Crawford (2004) highlighted the need for an ecosystem approach to fisheries management. A change to this approach is being adopted by government in an attempt

to reconcile resource utilisation and biodiversity conservation objectives (Hutchings *et al.* 2009). For most resources, the single species approach to management however still exists, with limited interactions between competing species or predators and prey being formally taken into account when modelling stock dynamics and providing management advice to authorities (Hutchings *et al* 2009). Linking seabird biology to these stock assessment models will be vital in ensuring the survival of marine top predators.

Lastly, while this paper has focused on adult penguins, it needs to be remembered that the survival of the species is also dependant on recruitment into the population of juvenile penguins. Fish larvae are often caught by juvenile penguins due to their inability to catch fast swimming prey (Wilson, 1985). Little is known on juvenile stage of the life history of the African penguin, nor the manner in which they interact with the pelagic fishery. More research is needed in this regard to ensure that the seabird biology of this species is adequately incorporated in the stock assessment models to ensure the survival of this species.

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Table 1: African Penguin adult moult and breeding figures from Dassen Island, Robben Island, Boulders, Stony Point, Dyer Island, St Croix Island and Bird Island. Data supplied by R Crawford, DEA. Dyer Island 2008 and 2009 were collected during this study.

	Adult Moulters							Breeding Adults					
Year	Dassen Island	Robben Island	Boulders	Stony Point	Dyer Island	St Croix Island	Bird Island	Dassen Island	Robben Island	Boulders	Stony Point	Dyer Island	St Croix Island
1984	–	–	–	–	–	–	–	–	48	–	10	39348	37056
1985	–	–	–	–	–	–	–	–	206	4	22	38154	38896
1986	–	–	–	–	–	–	–	–	454	9	54	36962	38904
1987	–	–	–	–	–	–	–	9176	952	14	82	31896	38911
1988	–	3457	–	–	–	–	–	13016	1698	68	110	26830	38919
1989	–	3392	–	–	–	–	–	16856	1658	76	138	21764	38926
1990	–	4730	–	–	–	–	–	17440	2556	108	178	16698	38934
1991	–	4915	–	–	–	–	–	18024	3758	262	154	12230	38941
1992	–	6538	–	–	–	–	–	15126	4054	316	114	15158	38949
1993	–	8002	564	–	–	8708	8708	14598	4352	482	80	4748	38956
1994	12360	7948	801	–	–	5659	5659	18778	5598	718	88	9298	37125
1995	12222	6563	1369	–	–	8514	8514	19584	4558	732	102	8520	35302
1996	12953	5608	885	–	–	7418	7418	19004	6194	832	116	6558	33479
1997	16296	8696	1031	–	–	9298	9298	17480	6672	1452	130	5490	31656
1998	10918	9397	2352	–	8415	–	–	21836	6934	1110	144	3926	29833
1999	25074	11765	2030	–	4564	–	–	30310	8798	1812	176	4726	28010
2000	26095	13317	3664	4545	4717	–	–	34084	11410	1898	208	4440	30422
2001	25619	13277	–	–	4216	–	–	42820	13446	2108	222	4176	33900
2002	22511	14737	–	–	5052	–	–	45362	14524	2166	234	4290	26066
2003	17592	17424	–	–	6177	–	–	40392	12890	2066	246	3858	18232
2004	18298	12871	–	–	3414	–	–	49802	17048	2392	196	4432	20176
2005	11350	7768	–	–	3348	–	–	45374	16420	2454	372	4106	8306
2006	7876	6496	–	–	2973	–	–	26566	8148	2150	530	4114	16154
2007	2312	5197	–	–	2807	–	–	23570	13538	1648	520	3026	8726
2008	442	3589	–	–	2420	–	–	11438	4484	1826	620	3210	15478
2009	–	3956	–	–	3313	–	–	10290	5294	–	–	–	13648
2010	–	–	–	4843	–	–	–	–	–	–	–	–	–

Table 2: Explanatory variables used in the regression analyses for predicting African penguin population sizes

	Notation	Variable	Years Data Available	Notes
1	Br_WC	Penguin breeders in the Western Cape		Dassen and Robben Islands, Boulders, Stony Point, Dyer Island
2	Br_EC	Penguin breeders in the Eastern Cape		St Croix and Bird Islands
3	Br_Das	Penguin breeders on Dassen Island	1985–2009	
4	Br_Rob	Penguin breeders on Robben Island	1984–2009	
5	Br_SP	Penguin breeders at Stoney Point	1984–2009	
6	Br_Bou	Penguin breeders at Boulders	1985–2009	
7	Br_Dy	Penguin breeders on Dyer Island	1984–2009	
8	Br_StC	Penguin breeders on St Croix	1984–2009	
9	Br_Bi	Penguin breeders on Bird Island	1984–2009	
10	M_Das	Penguin adults moulting at Dassen Island	1994–2009	
11	M_Rob	Penguin adults moulting at Robben Island	1988–2009	
12	M_Bou	Penguin adults moulting at Boulders	1993–2000	
13	M_SP	Penguin adults moulting at Stoney Point	2000	
14	M_Dy	Penguin adults moulting at Dyer Island	1998–2009	
15	M_StC	Penguin adults moulting at St Croix Island	1993–1997	
16	M_Bi	Penguin adults moulting at Bird Island	1993–1997	
17	Re_D_A	Anchovy recruits Stratum D	1985–2009	1987–no data
18	Re_E_A	Anchovy recruits Stratum E	1985–2009	1987–1990–no data
19	Re_D_S	Sardine recruits Stratum D	1985–2009	1987–no data
20	Re_E_S	Sardine recruits Stratum E	1985–2009	1987–1990–no data
21	Re_D_AS	Anchovy and sardine recruits Stratum D	1985–2009	1987–no data
22	Re_E_AS	Anchovy and sardine recruits Stratum E	1985–2009	1987–1990–no data
23	Sp_B_A	Anchovy Spawners Stratum B	1984–2009	1995–no data
24	Sp_C_A	Anchovy Spawners Stratum C	1984–2009	
25	Sp_E_A	Anchovy Spawners Stratum E	1984–2009	1984 &1991–no data
26	Sp_B_S	Sardine Spawners Stratum B	1984–2009	1995–no data
27	Sp_C_S	Sardine Spawners Stratum C	1984–2009	
28	Sp_E_S	Sardine Spawners Stratum E	1984–2009	1984 &1991–no data
29	Sp_B_AS	Anchovy and sardine spawners Stratum B	1984–2009	1995–no data
30	Sp_C_AS	Anchovy and sardine spawners Stratum C	1984–2009	
31	Sp_E_AS	Anchovy and sardine spawners Stratum E	1984–2009	1984 &1991–no data
		Kilojoule terms		
32	Re_D_A_kJ	Anchovy recruits Stratum D	1985–2009	1987–no data
33	Re_E_A_kJ	Anchovy recruits Stratum E	1985–2009	1987–1990–no data
34	Re_D_S_kJ	Sardine recruits Stratum D	1985–2009	1987–no data
35	Re_E_S_kJ	Sardine recruits Stratum E	1985–2009	1987–1990–no data
36	Re_D_AS_kJ	Anchovy and sardine recruits Stratum D	1985–2009	1987–no data
37	Re_E_AS_kJ	Anchovy and sardine recruits Stratum E	1985–2009	1987–1990–no data
38	Sp_B_A_kJ	Anchovy Spawners Stratum B	1984–2009	1995–no data
39	Sp_C_A_kJ	Anchovy Spawners Stratum C	1984–2009	
40	Sp_E_A_kJ	Anchovy Spawners Stratum E	1984–2009	1984 &1991–no data
41	Sp_B_S_kJ	Sardine Spawners Stratum B	1984–2009	1995–no data
42	Sp_C_S_kJ	Sardine Spawners Stratum C	1984–2009	
43	Sp_E_S_kJ	Sardine Spawners Stratum E	1984–2009	1984 &1991–no data
44	Sp_B_AS_kJ	Anchovy and sardine spawners Stratum B	1984–2009	1995–no data
45	Sp_C_AS_kJ	Anchovy and sardine spawners Stratum C	1984–2009	
46	Sp_E_AS_kJ	Anchovy and sardine spawners Stratum E	1984–2009	1984 &1991–no data

Table 3: Regression models for the annual breeding populations of African penguins at Dassen Island in relation to explanatory variables (Table 2). AIC=Akaike Information Criteria

Notation Br_Das +	r^2	AIC	s.e	t	df	p
	November Spawner Biomass-Stratum B					
(Sp_B_AS_kJ) i-1	45.4	352	0.785	3.78	15	0.001
(Sp_B_AS) i-1	42.5	352	0.00593	3.58	15	0.002
(Sp_B_AS) i-1			0.00576	3.09	14	0.004
(Sp_B_AS) i-2	51.1	350	0.00575	1.9		0.039
(Sp_B_AS_kJ) i-1			0.776	3.11		0.004
(Sp_B_AS_kJ) i-2	53.8	350	0.774	1.94	14	0.034
	May Recruit Biomass-Stratum D					
Re_D_AS_kJ	*	362	1.85	0.96	15	0.177
Re_D_AS	*	362	0.0132	0.89	15	0.195
	November Stratum B and May – Stratum D					
Re_E_AS_kJ			1.24	-0.62		0.272
(Sp_B_AS_kJ) i-1			0.798	2.96		0.006
(Sp_B_AS_kJ) i-2	51.7	351	0.853	1.99	13	0.034
	November Stratum C and May Recruit Stratum E					
Sp_C_S	26.7	357	0.00575	2.61	15	0.010
Sp_C_A	*	362	0.00505	0.65	15	0.264
(Sp_C_S) i-1	16.5	359	0.00602	2.04	15	0.030
(Sp_C_A) i-1	*	362	0.00503	0.93	15	0.184
(Sp_C_S) i-1			0.00616	1.9		0.040
(Sp_C_A) i-1	14	360	0.00468	0.76	14	0.231
(Sp_C_AS_kJ) i-1			0.559	1.28		0.110
(Sp_C_AS_kJ) i-2	13.3	360	0.527	0.7	14	0.248
(Sp_C_AS_kJ) i-1	16.2	359	0.46	2.02	15	0.031
(Sp_C_AS) i-1	14.1	359	0.00349	1.9	15	0.038
Sp_C_AS_kJ	17.7	359	0.461	2.11	15	0.027
(Sp_WC_kj) i-1	41.2	353	0.325	3.49	15	0.002
Re_E_AS_kJ			1.85	-1.25		0.116
(Sp_C_AS_kJ) i-1	19.3	359	0.562	2.4	14	0.016
Re_E_AS_kJ	*	363	1.71	0.19	15	0.425
Re_E_AS	*	363	0.012	0	15	0.499
Re_DE_AS_kJ	*	362	1.21	0.75	15	0.232
Re_DE_AS	*	363	0.00855	0.56	15	0.294

i Same year as Breeding or moult census, i-1 Lagged by one year , $_{i-2}$ Lagged by two years

Table 4: Regression models for the annual breeding populations of African penguins at Robben Island in relation to explanatory variables (Table 2). AIC=Akaike Information Criteria

Notation: Br_Rob +	r^2	AIC	s.e	t	df	p
	November Biomass-Stratum B					
(Sp_B_AS) i-1			0.00342	1.13		0.138
(Sp_B_AS) i-2	*	353	0.00244	-0.59	15	0.283
(Sp_B_AS_kJ) i-1	1.5	351	0.422	1.13	16	0.139
(Sp_B_AS) i-1	0.1	352	0.00311	1	16	0.165
(Sp_B_AS_kJ) i-1			0.47	1.2		0.125
(Sp_B_AS_kJ) i-2	*	353	0.35	-0.47	15	0.321
	May Recruit-Stratum D					
Re_D_AS	*	352	0.00536	0.73	16	0.238
Re_D_AS_kJ	*	352	0.756	0.78	16	0.223
	November Stratum B and May Recruit Stratum D					
Re_D_AS_kJ			0.603	2.18		0.021
(Sp_B_AS_kJ) i-1			0.421	1.45		0.085
(Sp_B_AS_kJ) i-2	17.2	350	0.316	-0.79	14	0.222
	November Biomass-Stratum C					
(Sp_C_AS_kJ) i-1	49.1	340	0.14	4.17	16	<0.001
(Sp_C_AS) i-1	48.4	340	0.00106	4.12	16	<0.001
Sp_C_AS_kJ	23.7	347	0.17	2.51	16	0.012
Sp_C_S	14.8	349	0.00244	1.99	16	0.032
Sp_C_A	8.3	350	0.00187	1.6	16	0.065
(Sp_C_S) i-1	26.2	346	0.00222	2.66	16	0.009
(Sp_C_A) i-1	25.8	346	0.00173	2.63	16	0.009
(Sp_C_S) i-1			0.00193	2.62		0.010
(Sp_C_A) i-1	45.7	342	0.0015	2.6	15	0.010
(Sp_C_AS_kJ) i-1			0.152	2.4		0.015
(Sp_C_AS_kJ) i-2	61.1	336	0.139	2.44	15	0.014
	Recruit Biomass- Stratum E					
Re_E_AS	14	349	0.00429	1.94	16	0.035
Re_E_AS_kJ	16.4	348	0.601	2.08	16	0.027
Re_E_AS_kJ			0.617	0.11		0.457
(Sp_C_AS_kJ) i-1	45.8	342	0.184	3.11	15	0.004
	Combined November and May Strata					
(Sp_WC_kj) i-1	51	339	0.515	4.32	16	<0.001
Re_DE_AS	13	349	0.078	1.88	16	0.039
Re_DE_AS_kJ	15.6	349	0.434	2.04	16	0.029

i Same year as Breeding or moult census, i-1 Lagged by one year , $_{i-2}$ Lagged by two years

Table 5: Regression models for the annual breeding populations of African penguins at Boulders in relation to explanatory variables (Table 2). AIC=Akaike Information Criteria

Br_Bou +	r^2	AIC	s.e	t	df	p
	November Biomass-Stratum C					
(Sp_C_AS_kJ) i-1			0.0396	0.73		0.239
(Sp_C_AS_kJ) i-2	42.9	270	0.0363	2.49	14	0.013
(Sp_C_AS_kJ) i-1	23	274	0.0367	2.41	15	0.015
(Sp_C_AS) i-1	24.1	274	0.000274	2.47	15	0.013
Sp_C_AS_kJ	18	275	0.0379	2.13	15	0.025
Sp_C_S	*	279	0.000571	0.96	15	0.177
Sp_C_A	22.2	274	0.000392	2.36	15	0.016
(Sp_C_S) i-1	5.1	278	0.000541	1.36	15	0.097
(Sp_C_A) i-1	18.6	275	0.000396	2.16	15	0.024
(Sp_C_S) i-1			0.00051	1.06		0.156
(Sp_C_A) i-1	19.3	276	0.000403	1.91	14	0.039
	May Recruit-Stratum D					
Re_D_AS	*	279	0.00118	0.62	15	0.273
Re_D_AS_kJ	*	279	0.166	0.65	15	0.264
	November Stratum C and May Recruit Stratum E					
Re_E_AS_kJ			0.158	1.59		0.068
(Sp_C_AS_kJ) i-1	30.1	273	0.0451	0.96	17	0.177
	Combined B and C Strata					
(Sp_WC_AS_kj)i-1	18.3	275	0.0327	2.14	15	0.025
Re_DE_AS	23.2	274	0.000665	2.42	15	0.015
Re_DE_AS_kJ	24.7	274	0.0934	2.5	15	0.012
	November Biomass - Stratum B					
(Sp_B_AS_kJ) i-1	*	280	0.000693	0.18	15	0.431
(Sp_B_AS) i-1			0.000752	0.43		0.338
(Sp_B_AS) i-2	*	281	0.000537	-0.74	14	0.236
(Sp_B_AS_kJ) i-1	*	280	0.0948	0.27	15	0.396
	May Recruitment Stratum E					
Re_E_AS	29.6	273	0.000871	2.78	15	0.007
Re_E_AS_kJ	30.5	272	0.122	2.83	15	0.007
	November Stratum B and Recruit Stratum D					
Re_D_AS_kJ			0.126	2.95		0.006
(Sp_B_AS_kJ) i-1			0.0837	0.63		0.270
(Sp_B_AS_kJ) i-2	28.7	274	0.063	-1.26	13	0.115

i Same year as Breeding or moult census, i-1 Lagged by one year , $_{i-2}$ Lagged by two years

Table 6: Regression models for the annual breeding populations of African penguins at Stony Point in relation to explanatory variables (Table 2). AIC=Akaike Information Criteria

Br_SP +	r^2	AIC	s.e	t	df	p
	November Biomass-Stratum C					
(Sp_C_AS) i-1			0.0112	-0.71		0.245
(Sp_C_AS) i-2	*	213	0.0107	0.61	13	0.275
(Sp_C_AS) i-1	*	211	0.00912	-0.45	14	0.329
(Sp_C_AS) i-1	*	211	0.0000687	-0.28	14	0.392
Sp_C_AS_kJ	*	212	0.00935	0.17	14	0.432
Sp_C_S	1.4	210	0.00012	-1.1	14	0.144
Sp_C_A	6.1	209	0.0000906	1.4	14	0.091
(Sp_C_S) i-1	8.3	209	0.000113	-1.54	14	0.074
(Sp_C_A) i-1	*	211	0.0000919	0.73	14	0.240
(Sp_C_S) i-1			0.00114	-1.69		0.057
(Sp_C_A) i-1	8.9	210	0.0000876	1.04	13	0.158
	May Recruit-Stratum E					
Re_E_AS	7	209	0.000208	1.46	14	0.083
Re_E_AS_kJ	4.9	210	0.0297	1.33	14	0.102
	November Stratum C and May Stratum E					
Re_E_AS_kJ			0.035	2.19		0.026
(Sp_C_AS_kJ) i-1	16.9	208	0.0102	-1.74	13	0.053
	November Biomass Stratum B					
(Sp_B_AS_kJ) i-1	0.1	210	0.019	-1.01	14	0.165
(Sp_B_AS) i-1	*	210	0.00014	-0.99	14	0.170
(Sp_B_AS) i-1			0.000151	-0.79		0.221
(Sp_B_AS) i-2	*	213	0.000151	-0.43	13	0.337
	May Recruit-Stratum D					
Re_D_AS	*	212	0.000245	-0.15	14	0.441
	November Stratum B and May Stratum E					
Re_E_AS_kJ			0.0323	1.83		0.0455
(Sp_B_AS_kJ) i-1			0.0193	-0.73		0.2385
(Sp_B_AS_kJ) i-2	10	210	0.0213	-1.16	12	0.1345
	May Stratum D and E					
(RE_DE_ASkj)i-1	*	211	0.00758	-0.78	14	0.2245
Re_D_AS_kJ	*	212	0.0346	-0.17	14	0.4335
Re_DE_AS	*	211	0.000159	0.93	14	0.1855
Re_DE_AS_kJ	*	211	0.0228	0.83	14	0.2095

i Same year as Breeding or moult census, i-1 Lagged by one year , $_{i-2}$ Lagged by two years

Table 7: Regression models for the annual breeding populations of African penguins at Dyer Island in relation to explanatory variables (Table 2). AIC=Akaike Information Criteria

Br_Dy +	r^2	AIC	s.e	t	df	p
	November Biomass - Stratum C					
(Sp_C_AS) i-1			0.222	-0.36		0.363
(Sp_C_AS) i-2	0.8	308	0.211	-0.97	13	0.175
(Sp_C_AS_kJ)	1.2	307	0.184	-1.09	14	0.148
(Sp_C_AS) i-1	2.2	307	0.00137	-1.16	14	0.134
Sp_C_AS_kJ	*	308	0.19	-0.83	14	0.210
Sp_C_S	*	308	0.00258	-0.47	14	0.324
Sp_C_A	*	308	0.00197	-0.8	14	0.218
(Sp_C_S) i-1	*	309	0.00252	-0.37	14	0.358
(Sp_C_A) i-1	4.1	307	0.00185	-1.28	14	0.110
(Sp_C_S) i-1			0.00252	-0.17		0.432
(Sp_C_A) i-1	*	309	0.00194	-1.19	13	0.127
	May Recruit Stratum E					
Re_E_AS	13.2	305	0.00419	-1.81	14	0.046
Re_E_AS_kJ	13.6	305	0.59	-1.83	14	0.044
	November Stratum C and May Stratum E					
Re_E_AS_kJ			0.772	-1.37		0.098
(Sp_C_AS_kJ)	7	307	0.225	-0.06	13	0.478
	November Biomass - Stratum B					
(Sp_B_AS_kJ)	*	309	0.41	-0.11	14	0.459
(Sp_B_AS) i-1	*	309	0.00302	0.04	14	0.483
(Sp_B_AS) i-1			0.00315	0.25		0.402
(Sp_B_AS) i-2	*	310	0.00315	-1.01	13	0.167
	May Recruitment - Stratum D					
Re_D_AS	*	308	0.00503	-0.66	14	0.261
Re_D_AS_kJ	*	308	0.71	-0.65	14	0.264
	May Stratum D and E					
Re_DE_AS	13.2	305	0.00308	-1.81	14	0.046
Re_DE_AS_kJ	13.6	305	0.436	-1.83	14	0.044

i Same year as Breeding or moult census, i-1 Lagged by one year , i-2 Lagged by two years

Table 8: Regression models for the annual breeding populations of African penguins at St Croix Island in relation to explanatory variables (Table 2). AIC=Akaike Information Criteria

Br_StC	r2	AIC	s.e	t	df	p
(Sp_E_AS) i-1	*	232	0.00381	-0.36	9	0.363
(Sp_E_AS_kJ) i-1	*	232	0.462	-0.4	9	0.350
(Sp_E_AS) i-1			0.00581	-0.56		0.302
Re_l_AS	*	145	0.0332	0.35	6	0.373
(Sp_E_AS_kJ) i-1			0.688	-0.62		0.284
Re_l_AS_kJ	*	145	0.0331	0.38	6	0.362
(Sp_E_AS) i-1			0.00885	0.34		0.378
Re_l_AS			0.0339	0.48		0.333
(Sp_E_AS) i-2	*	145	0.00805	-0.95	6	0.206
(Sp_E_AS_kJ) i-1			1.04	0.16		0.440
Re_l_AS_kJ			0.0347	0.33		0.382
(Sp_E_AS_kJ) i-2	*	145	0.923	-0.8	6	0.243
(Sp_E_AS) i-1			0.00935	-0.4		0.365
Re_l_AS			0.0331	-0.06		0.478
(Sp_E_AS) i-2			0.00815	-0.3		0.395
Sp_E_AS	*	142	0.00567	1.34 T	6	0.157
(Sp_E_AS_kJ) i-1			0.984	-0.53		0.324
Re_l_AS_kJ			0.0306	-0.11		0.462
(Sp_E_AS_kJ) i-2			0.83	-0.32		0.390
Sp_E_AS_kJ	*	142	0.639	1.52	6	0.134

i Same year as Breeding or moult census, i-1 Lagged by one year , i-2 Lagged by two years

Table 9: Regression models for the annual breeding populations of African penguins at Bird Island in relation to explanatory variables (Table 2). AIC=Akaike Information Criteria

Br_Bi	r^2	AIC	s.e	t	df	p
(Sp_E_AS) i-1	10.4	251	0.000631	1.58	12	0.07
(Sp_E_AS_kJ) i-1	9.5	251	0.0791	1.54	12	0.076
(Sp_E_AS) i-1			0.00107	-0.01		0.498
Re_I_AS	*	123	0.0599	0.35	4	0.373
(Sp_E_AS_kJ) i-1			0.13	-0.01		0.496
Re_I_AS_kJ	*	123	0.0598	0.35	4	0.373
(Sp_E_AS) i-1			0.00184	0.87		0.224
Re_I_AS			0.0589	0.36		0.371
(Sp_E_AS) i-2	*	123	0.00161	-1.07	2	0.183
(Sp_E_AS_kJ) i-1			0.216	0.76		0.253
Re_I_AS_kJ			0.0805	0.39		0.363
(Sp_E_AS_kJ) i-2	*	123	0.186	-0.96	2	0.204
(Sp_E_AS) i-1			0.00603	-0.23		0.420
Re_I_AS			0.307	-0.45		0.349
(Sp_E_AS) i-2			0.00389	0.02		0.492
Sp_E_AS	*	124	0.00629	0.53	2	0.325
(Sp_E_AS_kJ) i-1			0.541	-0.25		0.412
Re_I_AS_kJ			0.246	-0.5		0.333
(Sp_E_AS_kJ) i-2			0.341	-0.03		0.489
Sp_E_AS_kJ	*	124	0.607	0.62	2	0.299
(Sp_E_AS) i-1			0.000887	2.13		0.029
(Sp_C_AS) i-2	16.6	251	0.0012	-1.38	11	0.098
(Sp_E_AS_kJ) i-1			0.12	2		0.036
(Sp_C_AS_kJ) i-2	14.2	251	0.168	-1.29	11	0.112
Sp_E_S	5.7	252	0.000988	1.34	12	0.103
Sp_E_S_kJ	5.7	252	0.000988	1.34		0.103
Sp_E_A	16.2	250	0.000984	1.88	13	0.043
Sp_E_A_kJ	16.2	250	0.000984	1.88	12	0.043
(Sp_E_S) i-1	3.9	252	0.000899	1.23	12	0.121
(Sp_E_S_kJ) i-1	3.9	252	0.000899	1.23	12	0.121
(Sp_E_A) i-1	12.1	250	0.00159	1.67	12	0.060
(Sp_E_A_kJ) i-1	12.1	250	0.00159	1.58	12	0.060

i Same year as Breeding or moult census, i-1 Lagged by one year , i-2 Lagged by two years

Table 10: Regression models for the annual breeding populations of African penguins in the Western Cape in relation to explanatory variables (Table 2). AIC=Akaike Information Criteria

Br_WC	r^2	AIC	s.e	t	df	p
	November Stratum B					
(Sp_B_AS_kj) i-1	12	377	0.856	1.82	16	0.04
(Sp_B_AS) i-1	11.4	377	0.00627	1.79	16	0.047
(Sp_B_AS) i-1			0.00681	1.32		0.103
(Sp_B_AS) i-2	10	378	0.00487	0.86	15	0.201
	Biomass Stratum C					
(Sp_C_AS_kJ) i-1	28	373	0.357	2.76	16	0.007
(Sp_C_AS) i-1	26.9	374	0.0027	2.69	16	0.008
(Sp_C_AS_kJ) i-1			0.406	1.24		0.118
(Sp_C_AS_kJ) i-2	39.5	371	0.371	2.01	15	0.032
Sp_C_S	5.9	378	0.00549	1.44	16	0.085
Sp_C_A	–	380	0.00427	0.58	16	0.287
(Sp_C_S) i-1	17.8	376	0.00503	2.17	16	0.023
(Sp_C_A) i-1	10	377	0.00409	1.7	16	0.054
Sp_C_AS_kJ	4	378	0.409	1.31	16	0.105
(Sp_C_S) i-1			0.00491	1.97		0.034
(Sp_C_A) i-1	23.8	375	0.00382	1.5	15	0.078
	Recruitment Stratum E					
Re_E_AS	*	380	0.01	0.79	16	0.22
Re_E_AS_kJ	*	379	1.42	0.92	16	0.186
	Recruitment Stratum D					
Re_D_AS_kJ	*	380	1.65	-0.03	16	0.487
Re_D_AS	*	380	0.0117	-0.11	16	0.458
	Biomass Stratum C and Recruitment Stratum E					
Re_E_AS_kJ			1.54	-0.78		0.224
(Sp_C_AS_kJ) i-1	26.2	375	0.46	2.62	15	0.010
Re_E_AS_kJ			1.35	0.87		0.199
(Sp_C_AS_kJ) i-1			0.942	1.33		0.102
(Sp_C_AS_kJ) i-2	9.9	379	0.706	0.82	14	0.213
	Biomass Combined Stratum B and C					
(Sp_BC_AS_kj) i-1	39.8	370	0.283	3.5	16	0.002
	Recruitment Combined Stratum D and E					
Re_DE_AS	*	380	0.00726	0.49	16	0.315
Re_DE_AS_kJ	*	380	1.03	0.63	16	0.269

i Same year as Breeding or moult census, i-1 Lagged by one year , $_{i-2}$ Lagged by two years

Table 11: Regression models for the annual breeding populations of African penguins in the Eastern Cape in relation to explanatory variables (Table 2). AIC=Akaike Information Criteria

	r^2	AIC	s.e	t	df	p
(Sp_E_AS) i-1	*	243	0.00228	-0.43	10	0.339
(Sp_E_AS_kJ) i-1	*	243	0.276	-0.47	10	0.323
Re_I_AS	*	136	0.0161	-0.29	5	0.392
Re_I_AS_kJ	*	136	0.0161	-0.29	5	0.392

i Same year as Breeding or moult census, i-1 Lagged by one year , $_{i-2}$ Lagged by two years

Table 12: Regression models for the adult moulters of African penguins at Dassen Island, Robben Island, Dyer Island in relation to explanatory variables (Table 2). AIC=Akaike Information Criteria

M_Das +	r^2	AIC	s.e	t	df	p
(Sp_B_AS) i-1	32.4	286	2.69	2.69	12	0.010
Sp_B_AS	22.8	288	0.00603	2.2	12	0.024
Sp_B_AS_kJ	24.5	287	0.809	2.28	12	0.021
Sp_C_AS	17.7	309	0.00271	2	13	0.033
Sp_C_AS_kJ	19.1	309	0.361	2.08	13	0.029
M_Rob +						
Sp_C_AS			0.0013	1.51		0.076
(Sp_C_AS) i-1	45.4	362	0.00128	2.3	16	0.018
Sp_C_AS_kJ			0.162	1.86		0.041
(Sp_C_AS_kJ) i-1	52.4	359	0.159	2.54	16	0.011
(Sp_C_AS) i-1	41.4	362	0.00109	3.7	17	0.001
Sp_C_AS	31.6	365	0.00119	3.05	17	0.004
(Sp_B_AS) i-1	20.5	348	0.00287	2.32	16	0.017
M_Dy +						
Sp_C_AS	*	193	0.000828	0.57	9	0.29
Sp_C_AS			0.00102	0.23		0.413
(Sp_C_AS) i-1	*	195	0.001	0.46	8	0.329
Sp_C_AS_kJ			0.131	0.37		0.361
(Sp_C_AS_kJ) i-1	*	194	0.13	0.53	8	0.305
Sp_C_AS			0.000951	-0.03		0.487
(Sp_C_AS) i-1			0.0011	1.26		0.124
(Sp_C_AS) i-2	0.1	194	0.000858	-1.55	7	0.083
(Sp_C_AS) i-1	*	193	0.0081	0.72	9	0.246

i Same year as Breeding or moult census, i-1 Lagged by one year , $_{i-2}$ Lagged by two years

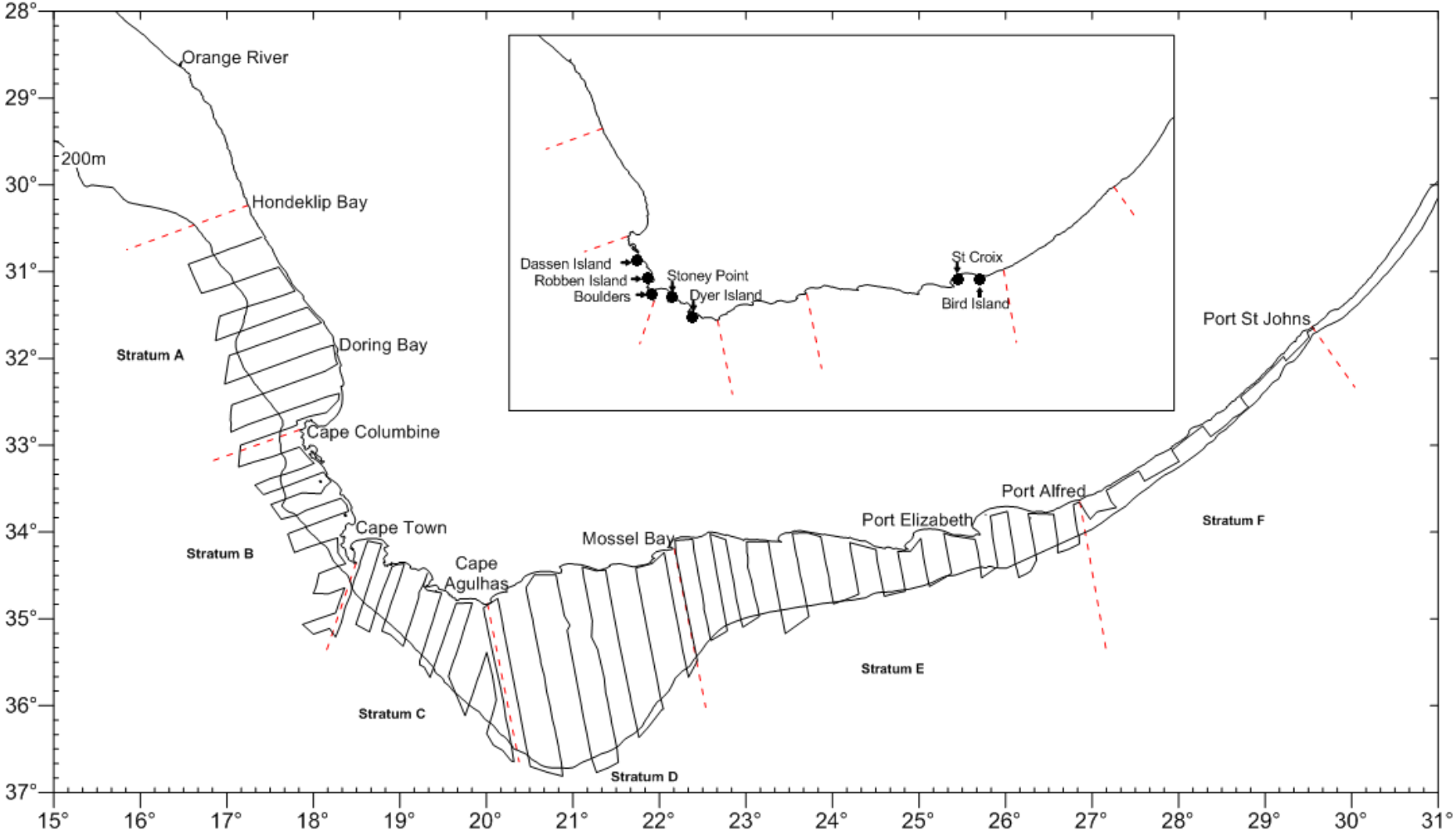


Figure 1: Tracks followed during the hydro-acoustic surveys during the November spawner biomass survey. The pre-defined strata used to split the coastline are indicated (red dotted lines), as is the 200m bathymetry line around the coastline (grey line). The insert shows the location of the African penguin breeding colonies referred to in the text and their location within the various strata. (Figure produced by Dagmar Merkle – DAFF)

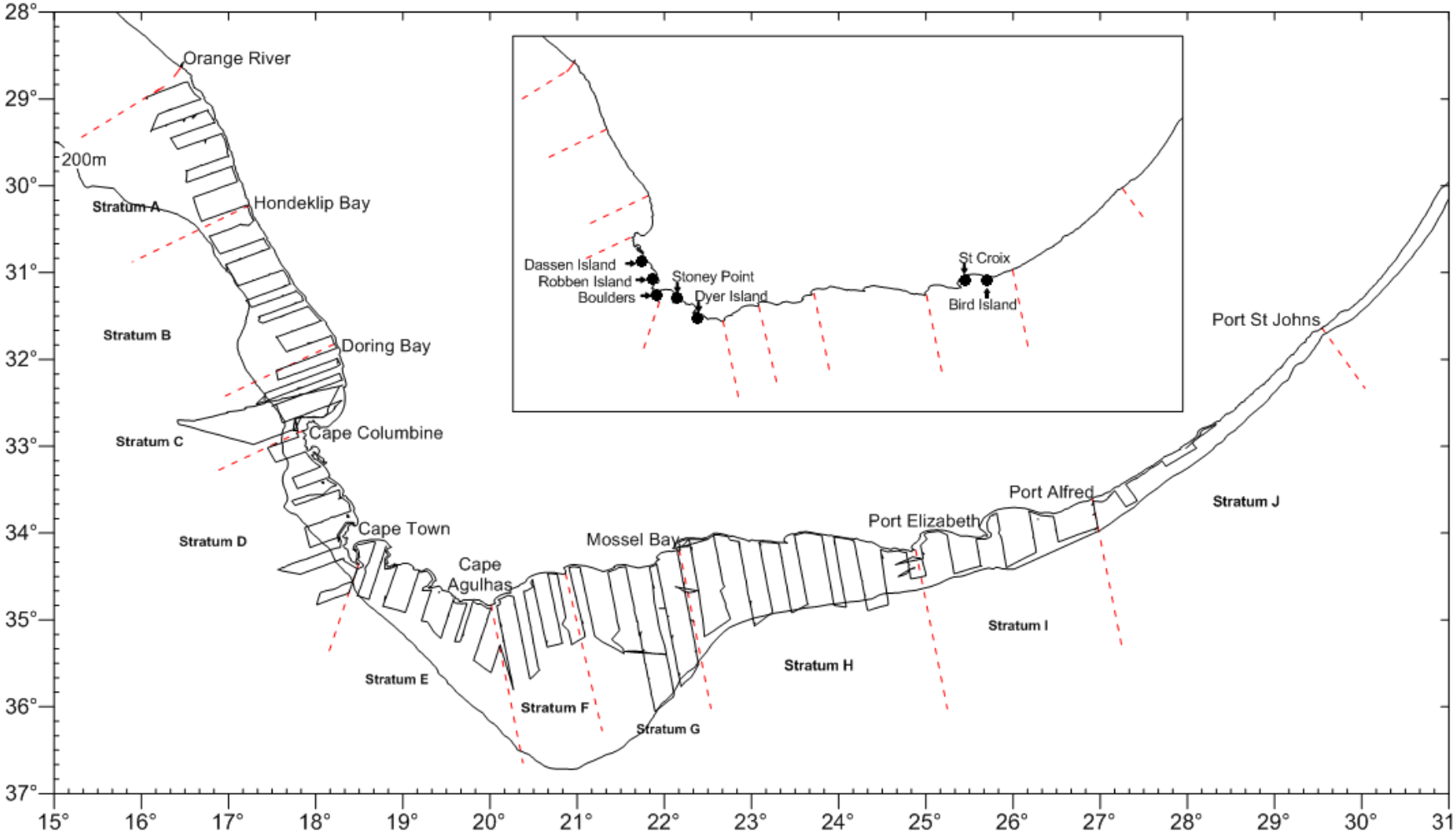


Figure 2: Tracks followed during the hydro-acoustic surveys during the May young-of-the-year- recruitment abundance survey. The pre-defined strata used to split the coastline are indicated (red dotted lines), as is the 200m bathymetry line around the coastline (grey line). The insert shows the location of the African penguin breeding colonies referred to in the text and their location within the various strata. (Figure produced by Dagmar Merkle – DAFF).

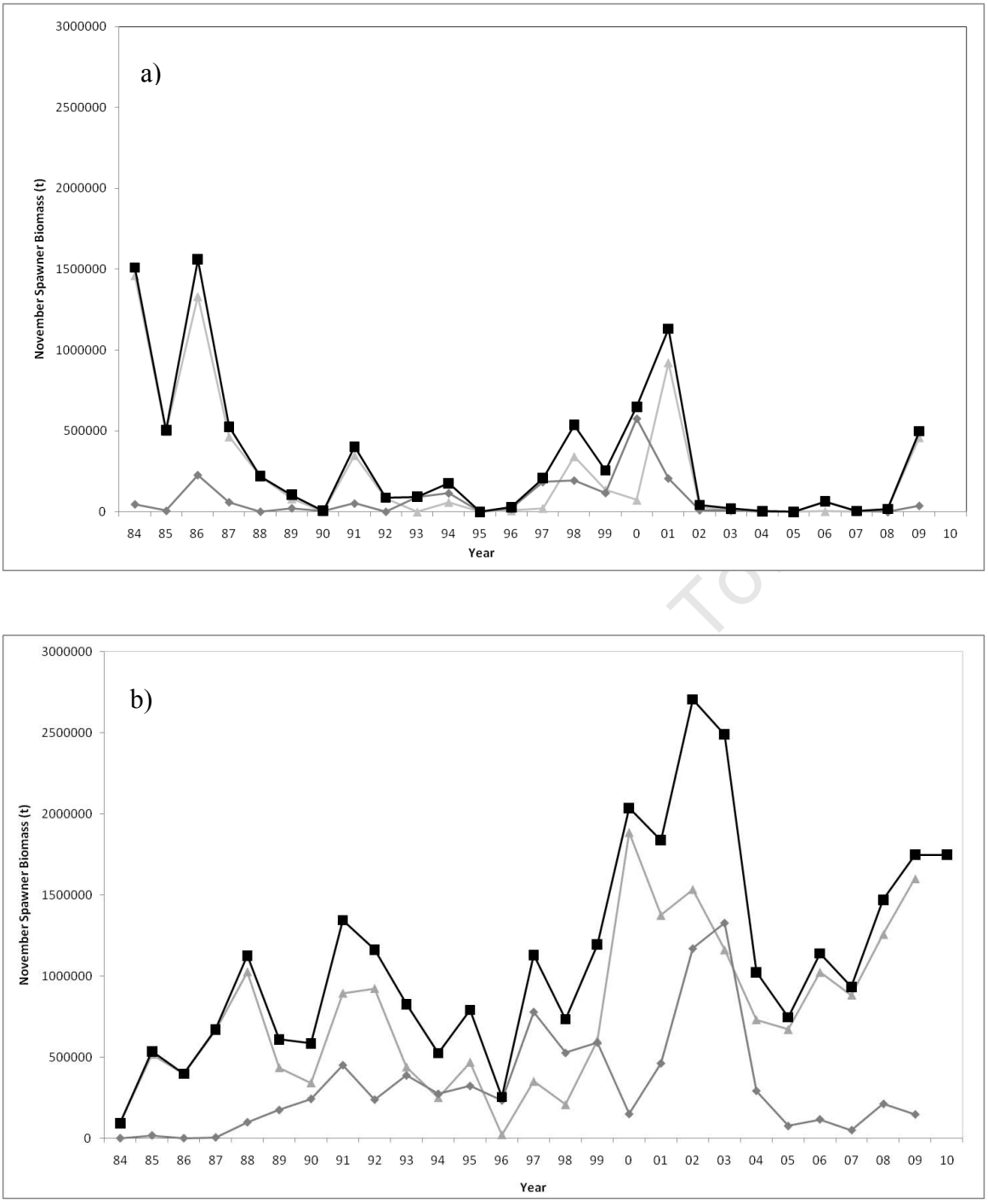
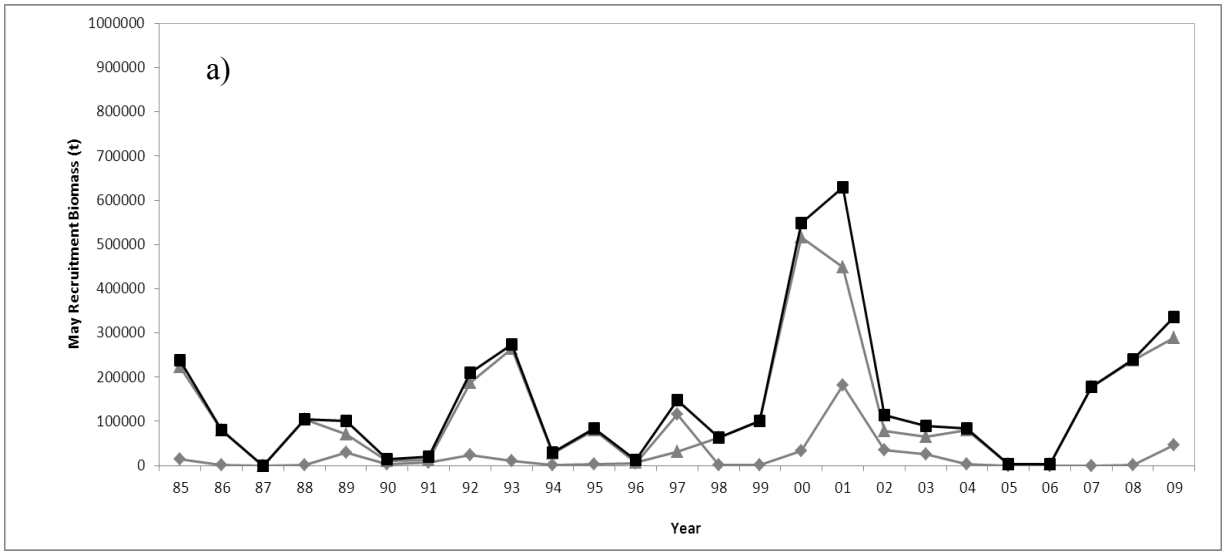


Figure 3: Time series of anchovy November spawner biomass (grey triangle), sardine November spawner biomass (grey diamond) and combined anchovy and sardine November spawner biomass (black square) in a) Stratum B, b) Stratum C



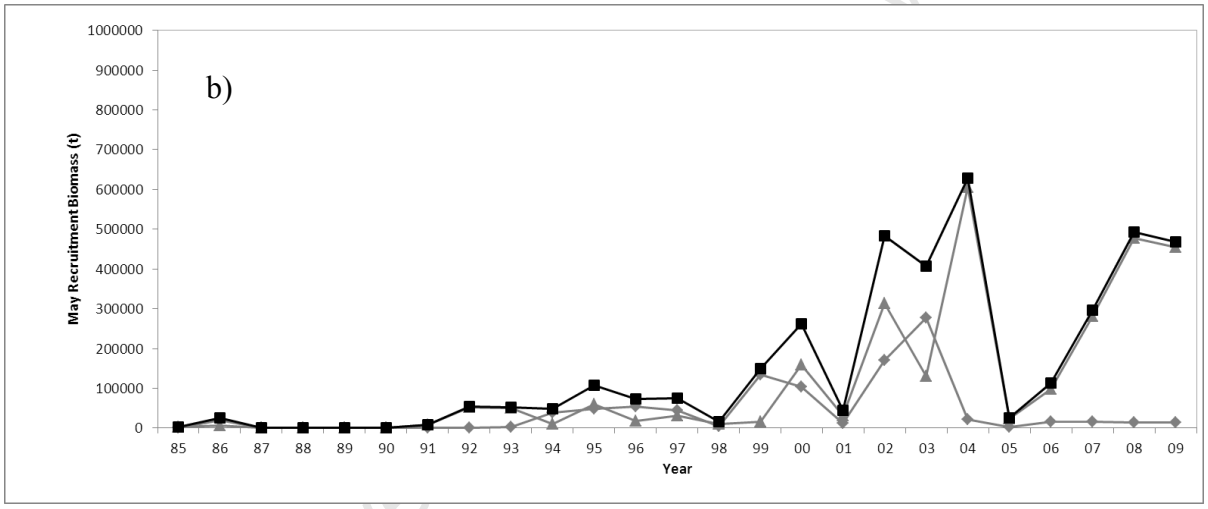


Figure 4: Time series of anchovy May recruitment biomass (grey triangle), sardine biomass (grey diamond) and combined anchovy and sardine biomass (black square) in a) Stratum D, b) Stratum E

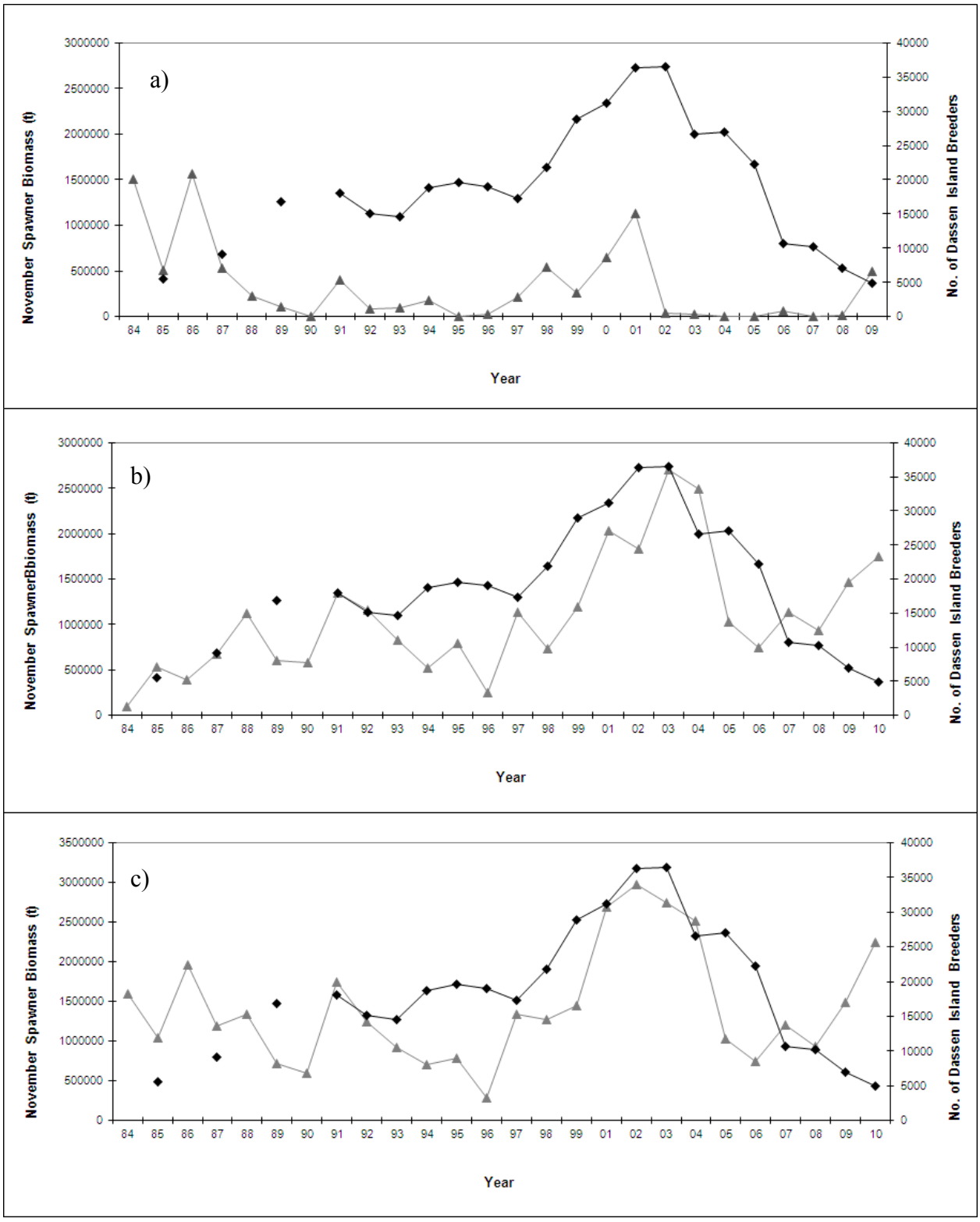


Figure 5: Relationship of Dassen Island breeders with a) Stratum B anchovy and sardine November spawner biomass b) Stratum C anchovy and sardine November biomass c) Stratum Band C anchovy and sardine November spawner biomass. Spawner biomass is grey triangles and number of penguins the black diamonds

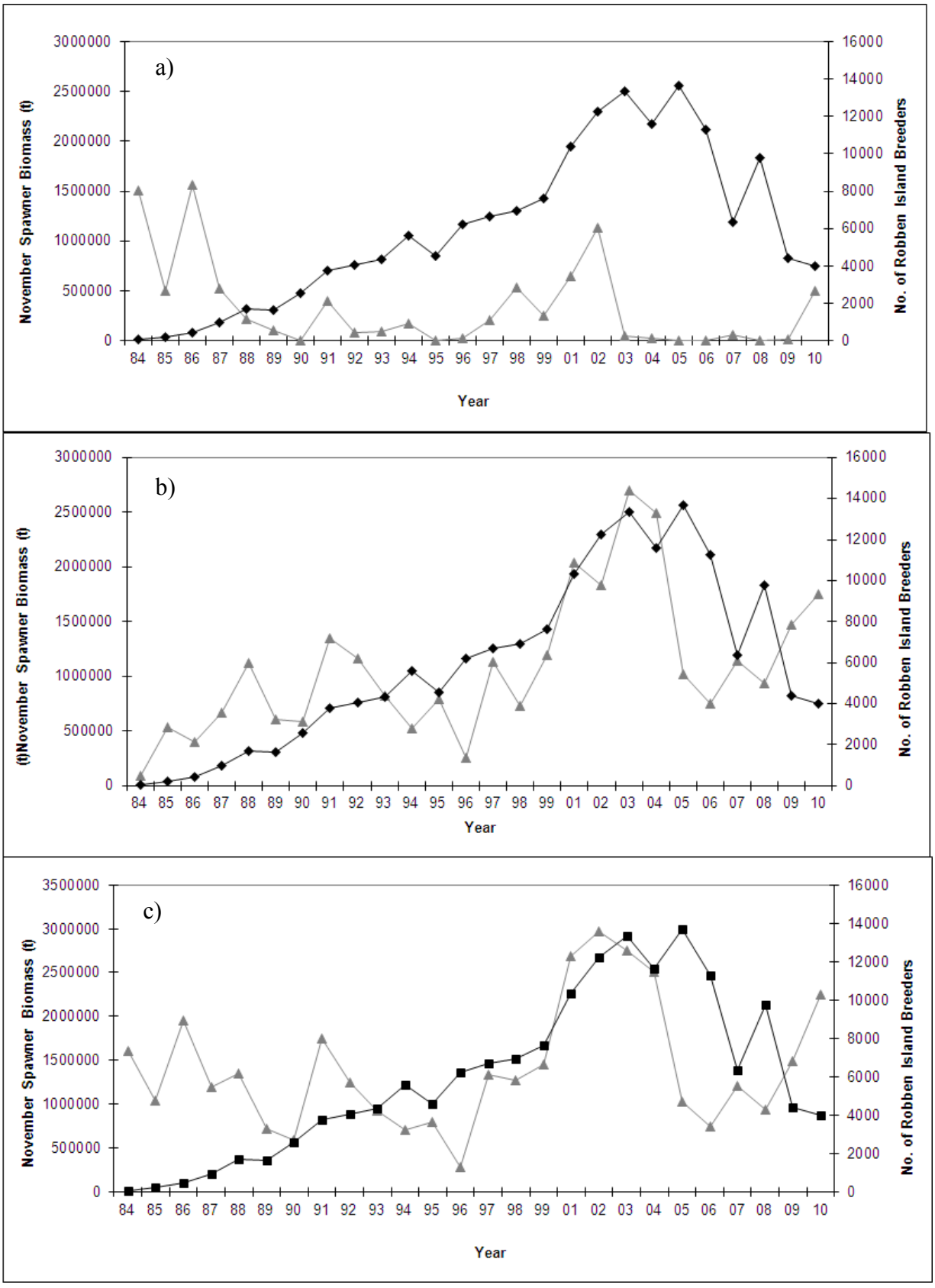


Figure 6: Relationship of Robben Island breeders with a) Stratum B anchovy and sardine November spawner biomass b) Stratum C anchovy and sardine November biomass c) Stratum B&C anchovy and sardine November spawner biomass. Spawner biomass is grey triangles and number of penguins the black diamonds

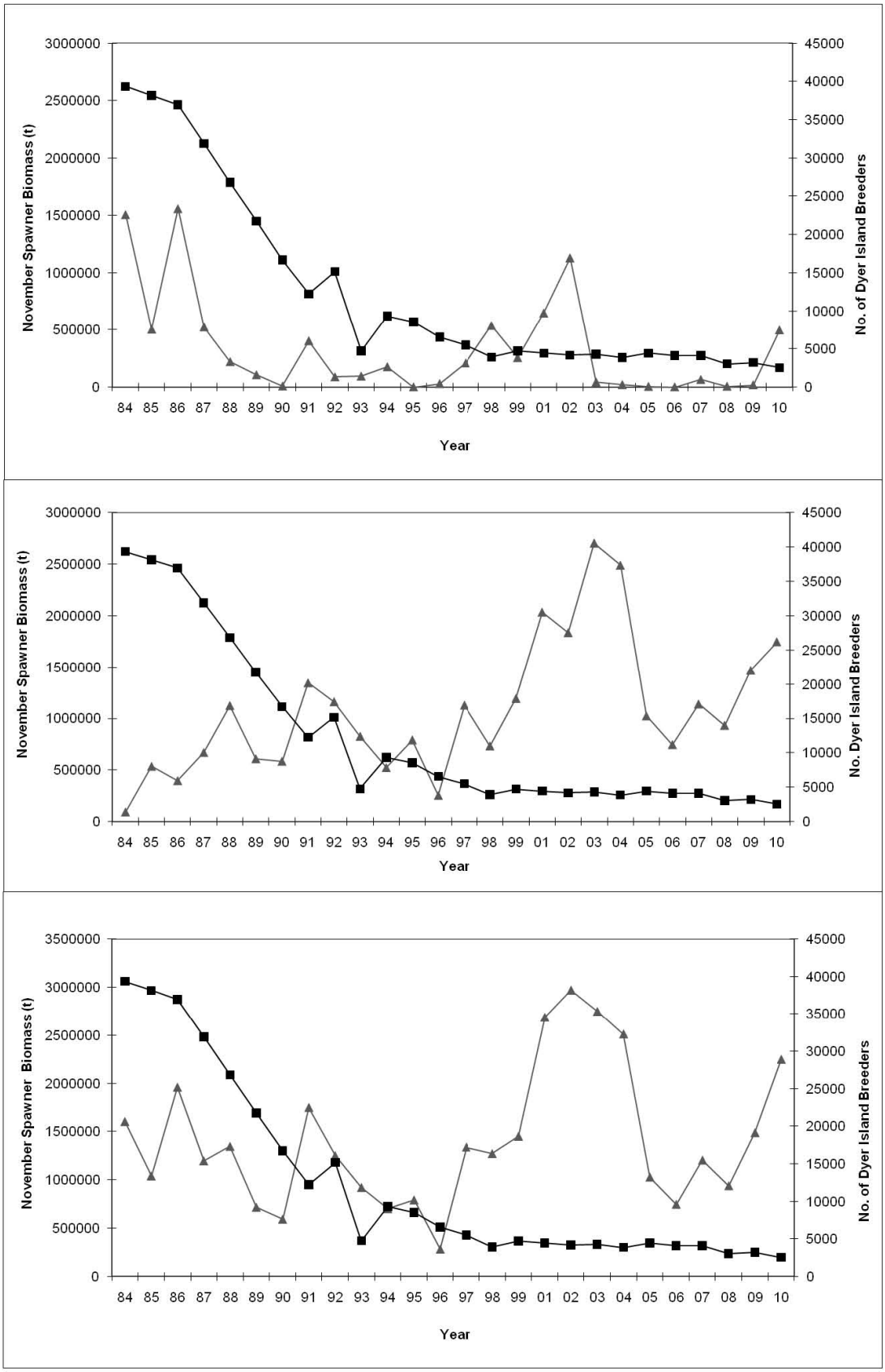


Figure 7: Relationship of Dyer Island breeders with a) Stratum B anchovy and sardine November spawner biomass b) Stratum C anchovy and sardine November biomass c) Stratum B&C anchovy and sardine November spawner biomass. Spawner biomass is grey triangles and number of penguins the black diamonds

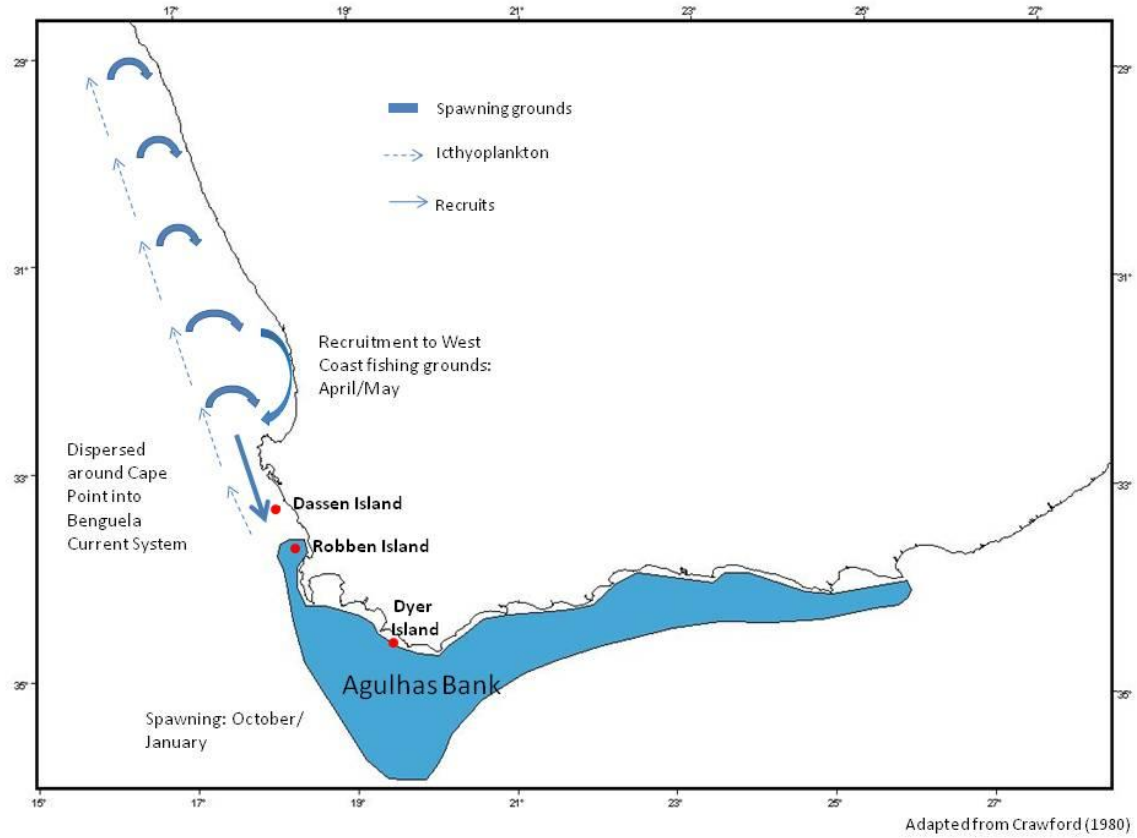


Figure 8: Simplified migration route of anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) in South Africa

CHAPTER 3

MOULT PHENOLOGY OF ADULT AFRICAN PENGUINS

Photo: L Waller

MOULT PHENOLOGY OF ADULT AFRICAN PENGUINS

ABSTRACT

Moult of African penguin *Spheniscus demersus* in adult plumaged birds from the four main breeding colonies in Namibia and six colonies in South Africa showed different patterns of seasonality. Moult seasonality was bimodal in Namibia, with a major peak in autumn, April-May and a minor peak in summer in December. Moult seasonality in South Africa was monomodal, with the major peak in summer, November/December. Moult at the South African colonies is more synchronous, with moult patterns at Dyer Island the most synchronous of all African penguin colonies. Moult counts are a more effective method of estimating a population size than nest counts. Given that there is movement of adults from their breeding colonies to moulting locations, moult counts need to be considered on a regional, as opposed to a colony scale, when interpreting population estimates based on moult counts. The number of adult-plumaged moulters has declined considerably in the Western Cape. Stony Point is an important moulting area for adult-plumaged African penguins in the Western Cape, although the numbers moulting at this colony do not account for the missing birds at the other colonies when comparing the ratio of adult moulters to breeders. Information derived from moult counts can provide an indication of areas that are considered more abundant in terms of food availability. An analysis of the juvenile moult patterns in South Africa is needed.

KEY WORDS

African penguin, moult, Namibia, South Africa, *Spheniscus demersus*, synchronicity

INTRODUCTION

Moult is a common phase shared in the annual cycle of all penguin species. It is an obligate process whereby all feathers are replaced annually, an essential feature for remaining waterproof and thus insulated in cold waters while

foraging (Stonehouse 1967, Payne 1972). Variation in the moult fast period ranges from 13–40 days depending on the species (Stonehouse 1967), with the inshore foraging species, occurring in lower latitudes, tending to have a shorter moult fast period than their offshore foraging, higher latitude counterparts (Croxall and Davis 1999). All penguins come ashore to moult where they can remain dry (Croxall 1982, Adams and Brown 1990), since moulting causes birds to lose their insulation and so cannot go to sea to feed (Groscolas and Cherel 1992, Davis and Renner 2003). Prior to moult they have to build sufficient reserves to both maintain basic metabolic processes, and to replace their entire plumage. Moult is thus a considerable energetically costly activity (Hoye and Buttemer in press), and in penguins, a unique process in which they replace their feathers in a short time period compared to that of flying birds which replace feathers gradually over many weeks (Kooyman *et al.* 2000, Hoye and Buttemer in press). This results in a high dependence on food availability by penguins at the time of moult (Kemper *et al.* 2008). The annual moult cannot safely be skipped. Penguins become hyperphagic during the pre-moult period (Otsuka *et al.* 2000), and the acquisition of sufficient body reserves during pre-moult foraging can be considered a greater priority than at any other stage of the annual cycle (Croxall and Davis 1999, Kooyman *et al.* 2000, Wolfaardt *et al.* 2009). Additionally, moult cannot be partial and it cannot be abandoned prematurely without compromising an individual's survival (Cooper 1978). Penguins are thus dependant on high and predictable food availability during the pre- and post-moult phases (Davis and Renner 2003, Wolfaardt *et al.* 2009). Penguins moult annually (Randall and Randall 1981, Randall *et al.* 1986, Kemper 2006) and this process generally occurs at a specific time of the year for each species (Croxall and Davis 1999). An understanding of timing of moult, including when and where pre and post-moult feeding takes place is of critical importance for penguin conservation management.

The annual moult of the adult African penguin *Spheniscus demersus* occurs subsequent to a c. 4 week pre-moult fattening up period (Randall and Randall 1981, Crawford *et al.* 2006a). Moult takes c. 3 weeks from arrival at the colony to departure, followed by a further c. 5–6 week recovery period after which breeding commences (Randall and Randall 1981, Kemper 2006). The moult period itself is classified into three phases; pre-feather shedding, feather shedding, and post-

feather shedding (Randall and Randall 1981). The feather shedding is the most distinctive, lasting on average 12.7 days (Randall *et al.* 1986). Until their first moult, the plumage of juvenile African penguins is distinct from that of adults, and the first moult replaces the juvenile plumage with the adult plumage. Therefore counts of adult-plumaged African penguins, made during the feather-shedding phase of moult, at 14-day intervals, and added over the year, provide an estimate of the number of penguins in adult plumage at a colony and region (Randall *et al.* 1986, Crawford *et al.* 1990, 1999, 2000, Crawford and Boonstra 1994, Kemper *et al.* 2001).

Moult is generally the most synchronous and seasonal aspect of the African penguin annual cycle in both Namibia and South Africa; at each colony it takes place at the same time of the year, but showing variation in timing between colonies (Underhill and Crawford 1999, Crawford *et al.* 2006a, Kemper 2006, Wolfaardt *et al.* 2009). The seasonal phenology of moult has been described for Dassen Island, Robben Island, Boulders, Bird and St Croix Islands in South Africa (Randall and Randall 1981, Wilson 1985a, Crawford *et al.* 1995a,b, 2006a, Wolfaardt *et al.* 2009). Hemming (2001) provided moult data for Stony Point for the 2000/01 moult season. In Namibia, the moult seasonality at Mercury Island, Ichaboe Island, Halifax Island and Possession Island was described by Kemper *et al.* (2007).

In the Namibian colonies, adult-plumaged penguins moult throughout the year, with peaks in April/May (Kemper 2006, Kemper *et al.* 2008). In the South African colonies, most adult-plumaged penguins moult from September to January, with moult reported to occur earlier in the Eastern Cape colonies (Bird and St Croix Islands), and latest in the Western Cape colonies of Robben and Dassen Islands (Crawford *et al.* 2006a) (Figure 1).

Adult African penguins usually moult at their breeding colony, although there is evidence to suggest that this is not always the case (Randall *et al.* 1987, Wolfaardt *et al.* 2008, Crawford *et al.* 2000, MFMR unpubl. data). While all adult penguins moult, not all adults breed. This is because (a) penguins in adult plumage are not necessarily of breeding age and (b) even those that are may not necessarily breed in a given year as a result of poor body condition for example.

If a greater number of adults are moulting than breeding, it is indicative of poor breeding conditions, or poor condition of breeding adults, because established breeders are abstaining from breeding (Crawford *et al.* 1999). Analysing moult and breeding trends per colony, can provide an indicator as to the trends of that local population, the relative health of the local ecosystem, as well as provide an indication as to the movement of individuals between colonies (Kemper *et al.* 2007).

This chapter provides a review of the moult phenology of adult African penguins throughout their distribution in Namibia and South Africa. It extends the results for patterns of moult of adult African penguins described by Underhill and Crawford (1999), Crawford *et al.* (2006a) and Wolfaardt *et al.* (2009) for South Africa and Kemper *et al.* (2007) and Kemper *et al.* (2008) in Namibia. Additionally, data for Boulders and Dyer, St Croix and Bird Islands are included. Population size and trends of penguins in adult plumage using moult counts and breeding populations are presented. Year to year variation in timing and synchrony of moult are considered, as are the inter-colony differences. Long-term trends in the timing and pattern of moult are evaluated. Understanding of timing and synchrony in moult is considered in light of management recommendations for various colonies.

METHODS

Adult moult counts

Counts of moulting African penguins at seven colonies in South Africa and at four colonies in Namibia (Figure 1) were available. The four Namibian colonies accounted for c. 97% of the total Namibian population (Table 1) (Crawford *et al.* 1995b, Kemper *et al.* 2007). Due to the length of time series, analyses were performed on five of the South African colonies, that of Dassen Island, Robben Island, Boulders, Dyer Island and Bird Island. These five South African colonies accounted for 81% of the estimated South African population (Crawford *et al.* in press).

Moult counts (see below) were made separately for immature and adult-plumaged birds; those for adult-plumaged penguins are considered in this

chapter. The fieldwork protocol is based on the estimate that penguins take c. 12.7 days to complete the feather-shedding phase of moult so counts every two weeks should therefore be of different penguins (Randall *et al.* 1986). Randall *et al.* (1986) suggested that the sum of two-weekly counts should provide an estimate of the number of penguins associated with a specific colony, assuming that most penguins moult every year at the colony at which they breed or intend to breed (Kemper *et al.* 2008). There is evidence to suggest however that this is not always the case (Randall *et al.* 1987, Wolfaardt *et al.* 2008, Crawford *et al.* 2000, MFMR unpubl. data). While all adult In some colonies, it is not logistically feasible to undertake the moult counts at exactly two-week intervals, and a more nuanced approach to estimation is described under Data analysis below. This algorithm also deals with the situation in which moult counts take place at, for example, weekly intervals.

Counts in the feather-shedding phase of moult were conducted at Robben Island at approximately two-week intervals from 1988 (Crawford *et al.* 1995a, 2006a, Underhill and Crawford 1999), at weekly intervals at Dassen Island from November 1994 until July 1999 and at two-weekly intervals from August 1999 to June 2010. On Dyer Island, counts were conducted every two weeks from September 1999–June 2007 (Crawford *et al.* 2006a). From 2007–2009 on Dyer Island, counts of moulting penguins were conducted weekly from November to January, in order to establish the peak moult date and period. Moult counts at the Namibian islands followed the standard two-weekly protocol (Kemper *et al.* 2007). At all three colonies, large groups of penguins (> c. 50 individuals) were counted twice, and if there was a substantial difference a third count was taken and the mean of the two closest counts adopted (Crawford and Boonstra 1994).

Although all African penguins moult annually, counts of adult plumaged moulting individuals will also include pre-breeders and non-breeders. Non-breeders can consist of established breeders which elected not to breed since their previous moult, or adult birds that don't breed, which may occur as a result of being physiologically compromised (eg Wolfaardt *et al.* 2008). Peak counts of active nests are therefore used to estimate the size of the breeding population (Shelton *et al.* 1984, Crawford *et al.* 1990, 1995a, 1995b, 2001, Crawford and Boonstra 1994, Kemper *et al.* 2001) but this has been shown to underestimate the

true number of breeding pairs (Kemper 2007, Wolfaardt *et al.* 2009) (see Discussion).

Active nest counts

African penguins in Namibia, and on Dassen Island, breed throughout the year (Wilson 1985a, Kemper 2006, Wolfaardt *et al.* 2008). Counts of active nests (those containing eggs or chicks) of African penguins are available from 1991 from Mercury Island, Halifax Island, Possession Island and from 1992 at Ichaboe Island in Namibia, all up to 2006 (Kemper 2006, Ministry of Fisheries and Marine Resources, Namibia). Counts were done monthly at Mercury Island since 1994, Ichaboe Island since 1992, Halifax Island since 1996 and twice monthly at Possession since 1996. Before then other counts exist but they were done "ad hoc" by Marine and Coastal Management, Department of Environmental Affairs South Africa, when they did their annual surveys, so were not necessarily at the peak.

At the South African colonies, regular annual counts of active nest sites have been conducted since 1987 (Underhill *et al.* 2006). An active nest site in this context was considered those nests containing eggs or chicks or defended by an adult, or contained signs of nest-building activity (Crawford *et al.* 1990, Wolfaardt *et al.* 2009). These were available at Dassen Island, Robben Island and Boulders from 1988 to 2009, at Dyer Island from 1990 to 2009 and at Stony Point, St Croix and Bird Islands (1993–1996) (Tables 2 and 3) (Crawford *et al.* 1990, 1995a, 1995b, 2001, Underhill *et al.* 2006, Wolfaardt *et al.* 2009). Counts were conducted from February to September each year in South Africa (Crawford *et al.* 1990). I consider how the active nest counts compare with the moult counts. Nest counts were multiplied by two to represent number of breeders, which makes for easier visual comparison with the moult data (*contra* Wolfaardt *et al* 2009). Based on measurements of breeding success and assuming an age at first breeding of four years (Whittington et al. 2005c) and a first-year survival rate of 0.51 p.a., survival of adult African penguins would need to be of the order of 0.85 p.a. to maintain a population in equilibrium (Crawford *et al.* 2006b). Thus, in a stable population of adult-plumaged penguins, with a survival rate of 85% per year; with all birds assumed to start breeding in their fourth year (Whittington *et al.* 2005c); with all breeding birds assumed to breed every year

and with all birds assumed to moult at the colony where they breed, the ratio between the sizes of the population of adult-plumaged birds (estimated from the moult counts) and the population of breeding birds (estimated from the nest counts) can be shown to be 1.38.

Data Analysis

For both South African and Namibian colonies, the moult year was split over two calendar years; the split was defined as the midpoint of the period in which fewest birds moulted; in South Africa the moult year was 1 July to 30 June and in Namibia from 1 September to 31 August (Randall *et al.* 1986, Underhill and Crawford 1999, Crawford *et al.* 2006a, Kemper *et al.* 2008). These split moult-years were designated by the year in which the peak moult period occurred; in South Africa, peak moult is in November–December and in Namibia the main peak moult period is in April–May (Crawford *et al.* 2006a, Kemper *et al.* 2008, Wolfaardt *et al.* 2009). Thus, following Wolfaardt *et al.* (2009) and Kemper *et al.* (2008), the 1988/89 moult year is designated 1988 for South Africa and 1989 for Namibia.

At each breeding colony, the moult counts were not done at uniform intervals. To compensate for this, linear interpolation was done between the actual counts to estimate the number of birds moulting each day (Underhill and Crawford 1999). These daily estimates were averaged over seven-day periods starting 1 July (for South African colonies) and 1 September (Namibian colonies) of each year and divided by 12.7, the average duration in days of the feather shedding period (Randall *et al.* 1986, Underhill and Crawford 1999). This provided the estimate of the number of birds reaching the mid-point of the feather-shedding phase of moult in each week (Underhill and Crawford 1999). The weekly moult estimates were summed to form annual estimates of the numbers of adult-plumaged penguins moulting at each colony in each moult year.

At each colony, the average overall pattern of moult phenology for adult penguins was calculated by summing the weekly totals over the years, and representing these as the percentage of birds moulting in each week (Underhill and Crawford 1999). Week 1 was defined as the week beginning 1 July for colonies in South Africa (Underhill and Crawford 1999, Wolfaardt *et al.* 2009), and 1 September for

colonies in Namibia (Kemper *et al.* 2008). For each year at each colony, the week at which the cumulative 20%, 50% and 80% of the birds had moulted was calculated. The number of weeks it took between the cumulative 20% and 80% mark, was used to calculate the number of weeks it took 60% of the birds to moult. This was used to evaluate moult synchrony patterns between the colonies.

I tested whether the timing of moult had changed through time, using the colonies for which at least eight years of moult count data were available. Regression models were fitted with year as explanatory variable and each of four dependent variables: the weeks of the year at which 20%, 50% and 80% of the penguins were estimated to have started moult in each year for which data were available, and the length of the interval within which the central 60% of penguins moulted, which measures the synchrony of moult.

RESULTS

Trends in numbers of adult-plumaged penguins based on moult counts

The number of moulting African penguins in adult plumage decreased steadily in Namibia (Figure 2). An overall increase in adult moulters was seen from 1994 to 1996 yet steadily declined till 2006. There is evidence to suggest an overall increasing trend in adult moulters at all Namibian Islands since 2006 except for Ichaboe Island, which continues to decline (Figure 2). The population decreased between 1996 and 2005, but has shown a slight increase in 2006 and 2007 (Table 2). At all colonies, the number of moulting adults was lowest in 2007 (Table 2).

At the three colonies in South Africa for which the longest time series were available, sharp declines occurred in numbers of adult moulters from 2001 at Dassen Island and from 2003 at Robben Island. A continued gradual decline was observed at Dyer Island since counts began in 1998 (Figure 3). During the final years of the study period, with the exception of the colony at Stony Point, the number of breeding pairs declined at all colonies in South Africa (Table 3).

Moult phenology

Moulting took place throughout the year in the Namibian colonies (Figure 4). The largest proportion of moulting took place between 19 April and 2 May (autumn) with a secondary peak in December/January (summer) (Figure 4). The proportion of penguins moulting during the week when most penguins moulted ranged between 3.1% at Possession Island and 6.1% at Mercury Island (Table 4). The cumulative number of birds that had moulted increased steadily throughout the year (Figure 6). In the six week period around the peak for each island, Mercury Island was the most synchronous with 32.9% (week 32–37) of all adult birds having moulted, with Possession Island the least synchronous with 17.4% birds having moulted (Table 4, Figure 6).

At the South African colonies, peak moult occurred in summer, ranging from the first week in November (Dyer Island) to the second week in December (Bird Island). The proportion of birds moulting during the week of peak moult ranged from 6.5% at Dassen Island, to 15.1% at Dyer Island (Table 4, Figure 5). In colonies in South Africa, few birds moult at the beginning and end of the moult year, with most adults moulting in a four month period between October and January (Figure 7). In the six week period around the peak for each island, Dyer Island was the most synchronous with 67.1% (week 16–21) of all adult birds having moulted; followed by Boulders at 59.6% (week 19–24); Robben Island at 50.9% (20–25); Dassen Island at 39.4% (19–24) and Bird Island at 37.5% (19–26) (Table 4, Figure 7).

The degree of synchrony in the moult phenology varied between years at all four colonies in Namibia (Tables 5 6, Figure 8). Mercury Island was the most synchronous, both in that the SD of mid date of moult was the smallest, and the mean duration of the mid 60% period was shortest of all Namibian colonies (Table 5, Figure 8). Possession Island in contrast had the largest values for both these measures (Table 5, Figure 8). With the exception of Ichaboe Island, from 2002/2003 to 2008/2009, there was a trend toward increasing moult synchrony, with the date by which 60% of adults had completed moult advancing earlier in the year (Table 6, Figure 8). The time it took for 60% of the adult birds to moult varied from 20.7 weeks at Mercury Island, to 24.2 weeks at Possession Island (Table 5).

In South Africa, adult moult phenology varied between years at all breeding colonies (Figure 9). The South African colonies were more synchronous than those in Namibia. At Dassen Island, the time it took for 60% of the adult penguins to moult varied between seven weeks in 2000 to 13 weeks in 2006 and 2007, with an average of 10.4 weeks (Table 5). At Robben Island, it took an average of 7.5 weeks for 60% of the adult birds to moult, and birds at Dyer Island had the most synchronous moult, with a mean of 5.5 weeks for 60% of the adult penguins to moult (Table 5, Figure 9).

Numbers of penguins moulting and breeding

The numbers of active nests fluctuated over the years for all colonies in Namibia, with an overall decreasing trend (Table 2). The maximum numbers of breeding pairs, for this series of data, were recorded in 1993 at Mercury Island, 1995 at Ichaboe Island, 1991 at Halifax Island, and 1993 at Possession Island. Conversely, the smallest number of breeding adults were recorded in 2007 for all sites, the last year for which counts are published (Table 4). In the South African colonies, the maximum number of breeding adults was recorded in 2004 for Dassen Island and Robben Island, 2005 for Boulders, 2009 for Stony Point, 1988 for Dyer Island, 1993 for St Croix and 2001 for Bird Island (Table 3). The lowest number of breeding adults were recorded in 2010 for Dassen Island, 1989 for Robben Island, 1988 for Boulders, 1993 for Stony Point, 2009 for Dyer Island, 2005 for St Croix and 2003 for Bird Island (Table 3).

In Namibia, the number of adult penguins moulting per 12-month period, and the maximum nest count of the following period were correlated at Ichaboe Island ($r=0.879$, $df=15$, $p<0.001$) and Possession Island ($r=0.789$, $df=10$, $p=0.004$) but not at Mercury Island ($r=0.205$, $df=15$, $p=0.447$) and Halifax Island ($r=0.525$, $df=10$, $p=0.119$). In South Africa, the number of adult penguins moulting per 12-month period, and the maximum nest count of the preceding year, were correlated at Robben Island ($r=0.767$, $df=20$, $p<0.001$) but not for Dassen Island ($r=0.373$, $df=13$, $p=0.188$) and Dyer Island ($r=0.256$, $df=10$, $p=0.448$). However, the number of adult penguins moulting per 12-month period, and the maximum nest count of the following year were correlated at Dassen Island ($r=0.749$, $df=13$,

p=0.002), Robben Island (r=0.916, df=21, p<0.001), and Dyer Island (r=0.750, df=10, p=0.008).

At the Namibian colonies, the estimates of the number of adult-plumaged moulters were greater than the number of breeders by a factor that ranged between 1.43 (in 1991) and 3.71 (in 1995) at Mercury Island; 1.43 (in 2003) and 3.5 (in 2004) at Ichaboe Island; 1.44 (in 1995) and 4.39 (in 2000) at Halifax Island; and 1.57 (in 2004) and 2.42 (in 1996) at Possession Island (Table 2). The mean ratios of adult-plumaged moulters to breeding adults were 2.61 (SD=0.70, n=16) at Mercury Island, 2.04 (SD=0.66, n=15) at Ichaboe Island, 2.84 (SD=0.8328, n=10) at Halifax Island and 1.95 (SD=0.28, n=11) at Possession Island (Table 2).

At the South African breeding colonies, the ratio of the number of adult-plumaged moulters to the number of breeders in the preceding breeding period ranged between a factor of 0.98 (in 1998) and 0.04 (in 2008) at Dassen Island; 2.05 (in 1989) and 0.44 (in 2007) at Robben Island; 0.72 (in 2006) and 2.14 (in 1997) at Dyer Island (Table 3). The mean ratio of adult moulters to breeding adults was 0.54 at Dassen Island (SD=0.29, n=15), 1.25 at Robben Island (SD=0.45, n=22) and 1.10 at Dyer Island (SD=0.41, n=12). For the three years in which data are available for Stony Point, the ratio adult-plumaged moulters to breeders were 21.85 in 2000, 4.48 in 2009 and 5.04 in 2010 (Table 3).

Eight colonies had at least eight years of moult count data. At six of the eight colonies, the length of the moult season increased (Table 6). Robben Island, with 21 years of data, had the longest time series of information, and is considered in more detail. Here, the interval during which 60% of the penguins moulted increased by 0.135 weeks/year (=0.94 days/year) (SE=0.059 weeks, t=2.28, df=19, p=0.034). Median 60%-moult interval in the first seven years of data was six weeks, and in the final seven years was eight weeks (Figure 9). At six of the eight colonies the date by which 20% of the penguins had started moult was earlier. On Robben Island, this date had become 0.179 weeks earlier per year (SE 0.060, t=2.99, df=19, p=0.007); the change was from a median of week 21 in the first seven years to a median of week 18 in the final seven years. At six of the eight colonies the date by which 50% of the penguins had started moult was

earlier. On Robben Island, this date had become 0.081 weeks earlier per year (SE 0.040, t=2.03, df=19, p=0.057); the change was from a median of week 24 in the first seven years to a median of week 22 in the final seven years. At seven of the eight colonies the date by which 80% of the penguins had started moult was earlier. On Robben Island, this date had become 0.044 weeks earlier per year (SE 0.038, t=1.15, df=19, p=0.263); the change, though not significant was from a median of week 27 in the first seven years to a median of week 26 in the final seven years (Table 6).

DISCUSSION

Population trends

Banding studies reported by Whittington *et al.* (2005a,b) showed that emigration of young birds from Namibia to South Africa is uncommon, and that permanent immigration from South Africa to Namibia is rare. African penguins in Namibia can thus be considered as a distinct regional population (Kemper *et al.* 2007), and so it is necessary to interpret Namibian and South African population trends of African penguins separately.

The decline of the African penguin in the 19th and 20th century has been well documented by Kemper *et al.* (2001, 2007). At the beginning of the 21st century, African penguins in Namibia bred on 14 islands and two mainland sites, yet by 2004, had ceased breeding on six islands (Kemper 2006, Kemper *et al.* 2007). Namibia was estimated to contribute one third of the global African penguin population when c. 100 000 African penguins were reported in the 1950s, during the first comprehensive surveys of penguin populations (Rand 1963a, Crawford *et al.* 1995b). This was considered to have already represented a significant decline from the middle of the 19th century, primarily due to African penguin egg collecting and guano scraping (Whittington *et al.* 2000, Kemper *et al.* 2001, 2007). Since the 1950s, the Namibian population declined by a further c. 75% during the second half of the 20th century (Kemper *et al.* 2001). Mercury Island and Ichaboe Island were the only colonies that supported more than 1000 breeding pairs by the early 1990s (Crawford *et al.* 1995a). Mercury Island was the only colony in 2004 with >1000 breeding pairs (Kemper et al. 2007).

The decrease in the Namibian African penguin population in the mid to late 20th century was primarily due to the guano exploitation and associated disturbance, as well as to scarcity of food (Frost *et al*. 1976, Cordes *et al*. 1999). The commercially exploited stocks of anchovy and sardine fish stocks collapsed in Namibia in the 1960s (Crawford and Shelton 1981, Crawford *et al*. 1985). The Lüderitz upwelling cell divides the northern and southern Benguela regions, resulting in a barrier to marine organisms and most pelagic fish stocks (Boyer and Hampton 2001, van der Lingen *et al*. 2006). Due to this oceanographic barrier, these stocks were unable to recover through recruitment from stocks originating in the southern Benguela. This resulted in the substantial decline of the African penguin in Namibia in the second half of the 20th century (Kemper *et al*. 2001). Furthermore, a large decline in adult plumaged birds was seen in 1993, this was driven by the decrease at Mercury Island, which Kemper *et al*. (2007) attributed to a seal disturbance programme at the colony. Oceanographic anomalies further contributed to declines. Unusually low levels of oxygen off central Namibia in 1994 caused fish mortalities and changes in fish distribution and in 1995, a Benguela *Niño* led to further declines in fish abundance (Kemper *et al*. 2001). Declines in the Namibian population continued into the 2000s, with c. 25 000 adult individuals estimated from moult counts in 2004 (Kemper *et al*. 2007). Results presented in this study suggest that the population may be stabilising at a low level, with 23 345 adult plumaged individuals counted moulting at the four most important Namibian colonies in 2007.

Following the collapse of the sardine stock in Namibia in the 1970s, bearded goby *Sufflogobius bibarbatus* became the main prey source of African penguins in Namibia (Crawford and Shelton 1981, Crawford *et al*. 1985). By 2010, anchovy and sardine stocks had seemingly not recovered in Namibia, because Ludynia *et al*. (2010) report that at Mercury Island (the largest African penguin breeding colony at the time of their study) the bearded goby was the main prey item of African penguins from 1996–2009 in both frequency of occurrence and mass. Because the energy content of the bearded goby is c. 40% that of sardine and anchovy, it is unlikely to be a preferred prey item of the African penguin (Ludynia *et al*. 2010). It appears that low prey quality rather than low prey abundance is a key factor influencing population dynamics of African penguins at Namibia (Ludynia *et al*. 2010).

Estimates of the number of African penguins in South Africa have indicated a large decline between the 1950s and the early 1980s, followed by a steady increase during the 1990s (Underhill *et al.* 2006, van der Lingen *et al.* 2006). From 2004 to 2009, the South African population has declined by a further 40%, from 52 481 breeding pairs in 2004 to 20 699 pairs in 2009 (Crawford *et al.* in press), and the numbers of adult plumaged moulting birds and numbers of breeders having reached the lowest numbers on record in 2010 (Crawford *et al.* in press). These declines resulted in the species being listed as Endangered according to the IUCN red data list (BirdLife International 2010). Apart from the small mainland colony at Stony Point, all South African colonies have declined in both adult plumaged moulters and numbers of breeders estimates. Reasons for this decline have been attributed to competition with commercial fisheries, and a mismatch between the penguin breeding colonies and their prey as a result of an eastward shift in their prey distribution (Fairweather *et al.* 2006, van der Lingen *et al.* 2006, Crawford *et al.* in press).

Moult counts as a population estimate tool

Moult is the process during which new feathers grow under the skin, extruding the old feathers as they emerge (Stonehouse 1967). In penguins, this process happens rapidly over 13–34 days (Adams and Brown 1990). The initiation of the process is difficult to observe in the field, hence moulting penguins are counted during the feather-shedding phase of the moult when the penguins are land-bound (Kemper 2007). In African penguins, the feather-shedding phase takes approximately two weeks, so moult counts need to be conducted at two-weekly intervals to ensure that all individuals are counted (Randall *et al.* 1986, Underhill and Crawford 1999, Kemper 2007). Accurate population size estimates at specific localities have been obtained using this method (Randall *et al.* 1986, Crawford *et al.* 1999, Kemper *et al.* 2001). Moult counts are interpolated linearly between actual counts to calculate the daily numbers of moulting birds (Underhill and Crawford 1999). These daily counts are then summed for the year. The total is divided by the average duration of the feather-shedding phase, defined as lasting from the day when the first feather is lost to the day the last feather is lost (Kemper 2007). The feather-shedding interval that has conventionally been used (Randall *et al.* 1986, Underhill and Crawford 1999, Kemper *et al*, 2001, 2008) is 12.7 days, based on a study of 45 birds at St Croix

Island (Randall 1983, Randall *et al*. 1986). Kemper (2007) noted the sensitivity of the moult count census method to estimates of the feather-shedding duration. If the feather-shedding duration was set one day longer for example, estimates at the four colonies in Namibia would be 7.3% lower. Furthermore, Weimerskirch *et al*. (1992) found that the length of the moult period in adult King penguins at Possession Island (Crozet Islands) varied according to the year and stage of the breeding season. If this is true for African penguins, then such changes in the feather-shedding duration would alter our interpretation of population trends and population estimates and would have important implications for conservation management planning (Kemper 2007). Crawford *et al*. (2007) documented an altered carrying capacity of the Benguela Upwelling Ecosystem for African penguin. If moult duration is impacted by available feeding conditions as Weimerskirch *et al*. (1992) suggested, the feather shedding duration of African penguins needs to be confirmed on an annual basis, particularly in the light of current poor feeding conditions across its range.

Number of adult plumage penguins moulting in relation to numbers breeding

To date, the recommendation made by Kemper (2007) to investigate the feather-shedding duration has not been investigated further. This is probably due to the labour intensive nature of the method, and the relative inaccessibility of some of the colonies, and the fact that there are relatively few banded individuals moulting in close proximity in the colonies (pers. obs). For the purposes of this discussion, the 12.7-day feather-shedding interval is used.

A concern in using the breeding nest count data is that African penguins have an extended breeding season (Wilson 1985a, Kemper and Roux 2005), and breeding is not well synchronised (Kemper 2006). At the peak time of breeding, only a portion of the breeding adults associated with a colony may actually be breeding (Kemper 2006). Additionally, not all sexually mature adult African penguins breed each year (Randall and Randall 1981, Whittington *et al*. 1996, Kemper 2006) and so the annual peak count may be an underestimate of the size of the breeding population (Kemper *et al*. 2008). In the absence of other, more reliable census methods to estimate breeding populations, counts of active nests or active nest sites are currently used to provide information on population estimates and

trends of African penguins and provide the best information to date on population estimates and trends on African penguins.

Because African penguins moult annually (Randall and Randall 1981), the number of moulters in a colony would be expected to be at least twice that of the number of active nests counted in the preceding year, because each active nest represents two adult penguins (Wolfaardt *et al.* 2009). If one adjusts the previously used convention however, and uses the number of moulters to breeding adults (active nests ×2), any figure below one would indicate more breeders than moulters (which would not make biological sense if adults moult at their breeding colony), and any figure higher than 1 would indicate that there are more moulters than breeding birds. This would be expected since there is a percentage of young birds in adult plumage that are not yet breeders. The larger the ratio of moulters to breeding birds however, the greater the number of non-breeders there are in the population. In a stable population (see Methods section), the ratio of adult plumaged moulters (i.e. birds at two years and above) to breeders (i.e. birds at four years and above) is 1.56. Any ratio above that may imply a higher proportion of established breeders that have elected not to breed.

The mean ratio of moulters to breeding adults in Namibia in this study was 2.49, similar to that reported by Kemper *et al.* (2007) of 2.43 (figure adjusted to reflect breeding adults). This means that there are twice as many adult-plumaged African penguins in Namibia than there are those that breed. It is important to look at these ratios per colony however, to prevent the overall mean masking what is occurring at individual colonies (Kemper 2007). The ratio of moulters to breeders at Halifax Island in 2006 seems to highlight this point, where the mean ratio was 3.35. This could be breeders from other colonies that moult at Halifax that then go back to their breeding colonies or young birds settling on Halifax, as per Kemper *et al.* (2008), which may suggest better feeding conditions at Halifax during the pre-moult fattening.

Crawford and Boonstra (1994), in their study at Robben Island, found that the number of moulting adults was greater than the maximum active nest sites by a mean factor of 3.2 (or 1.6 for number of breeders) for the years between 1988 and 1993, a period at which time the colony was growing. Wolfaardt *et al.* (2009), found a mean difference between number of adult moulters and breeders to be

0.64 at Dassen Island (1994–2005) and 1.36 at Robben Island (1988-2005) (ratio adjusted to reflect moulters to breeding birds, and not moulters to breeding pairs as reported in Wolfaardt *et al.* 2009). During the course of this study, the ratio had declined to 0.04 at Dassen Island (1994–2008) to 1.25 at Robben Island (1988–2008).

A reduction in the ratio between counts of adult moulters and nest sites can suggest an increase in the proportion of the adult population attempting to breed (Wolfaardt *et al.* 2009). However, from 1994–2009 at Dassen Island the ratio of moulters to breeders was <1, and from 2004 and 2009 it was <1 and at Robben Island. These ratios imply that there are 'missing birds,' not enough to account for the number of adults recorded breeding, with no allowance made for any pre-breeders in adult plumage in the population. Wolfaardt *et al.* (2009) stated that the moult counts at Dassen Island and Robben Island may be underestimated. At Dassen Island and Robben Island, moult counts are focused along the coastline, but substantial numbers of penguins are known to moult inland (Wolfaardt *et al.* 2008, NJ Parsons pers. comm.) that are not being included in the coastal moult counts. From banding data, Wolfaardt *et al.* 2008 estimated that 32% of penguins on Dassen Island were moulting away from the coast. Using this estimate for 2009, the year of the last moult count available at Dassen Island, this would change the number of moulters of 442 to 575, and the ratio of moulters to breeding birds to 0.05, still not enough to account for at least one moulter to one breeding bird at Dassen Island.

African adult penguins generally moult at their breeding colony (Randall *et al.* 1987, Wolfaardt *et al.* 2008). There are records however of birds moulting at colonies other than those at which they breed (Crawford *et al.* 2000, Whittington 2002, Whittington 2005c), which makes it more difficult to interpret the moult counts (Wolfaardt *et al.* 2009). Certainly observations at the Stony Point colony would indicate this. Hemming (2001) counted more birds moulting in adult plumage in 2000 at this colony than would be expected from their breeding numbers, and the 2010 estimate of moulting birds at Stony Point show that the ratio of moulters to breeders is 5.2, the highest of all the South African colonies. It is possible that these are some of the breeders from Dassen Island and Robben Island. Stony Point is close to the Agulhas Bank, the main spawning area for

anchovy and sardine, and an area that Wolfaardt *et al.* (2008) consider an important foraging area for pre-moult African penguins from the Western Cape. For Robben Island specifically, there are strong relationships between the number of moulters on that island and the pelagic spawner biomass in the area in which Stony Point is found, suggesting this is indeed an important pre-moult and post-moult area for African penguins (Chapter 2).

At Dyer Island, approximately 60 km away from Stony Point, the ratio of moulters to breeders was higher in 2009 compared to that recorded since 2004, although lower than that at Stony Point. This may suggest that an increase in breeding participation. However the number of breeding adults declined in 2009, suggesting that the increased number of moulters there are either breeders from other colonies or non-breeders.

It is unlikely that the penguins moulting in the inland areas of Dassen Island and Robben Island that are omitted from the moult counts, and the penguins that are moulting at colonies other than that at which they breed, would account for the thousands of birds that represent the decline in overall breeding numbers in South Africa. Moulting counts are not available at all the South African colonies, yet from 2004–2009, the number of breeding pairs declined from c. 39 900 to 12 600 at the seven main breeding colonies, a decline of c. 27 200 pairs, which is at least 54 000 moulters (excluding non breeding birds). While there are occasional reports of South African banded penguins that are sighted in Namibia, the number of moulting adults or breeding birds in Namibia has not increased to the extent that would account for the missing South African birds.

Boersma (1978) stated that if breeding strongly reduces an individual's chance of moulting successfully, moulting should precede breeding, or breeding skipped entirely, and that moulting as a prelude to breeding is an adaptation to unpredictable fluctuations in marine productivity associated with marine upwellings. Wolfaardt *et al.* (2009) found that the number of adult penguins moulting per 12-month period and the maximum nest count for the preceding period was correlated at Robben Island, but not for Dassen Island. In this study however, the maximum nest count was significantly correlated with the number of adult moulters of the previous year at Dassen Island, Robben Island and Dyer

Island. This suggests that it is the quality of the moulting period, primarily measured as the availability of food to achieve sufficient pre-moult condition, that not only determines the penguin's decision to breed the following season, but also their survival into the next breeding season.

Penguins need to lay down sufficient fat reserves before coming ashore to survive the 21-day fast and the requirements of growing a whole new set of feathers at once (Cooper 1978). Pre-moult increases of 31% in weight have been reported by Cooper (1978) for African penguins. During moult, African penguins loose up to 41% of their body mass (Cooper 1978) and it essential that they have access to a predictable supply of food close by. It is possible that penguins which reach too low a mass cut short their moult, by going to sea when not all the old feathers have been replaced, although they are then unlikely to survive (Boersma 1975, Cooper 1978, Rand 1960). Fasting and regenerating new feathers reduces the size of the pectoralis and supracoracoideus muscles (Wilson 1985b), the principal swimming muscles (Schreiweis 1982). Freshly moulted penguins have reduced swimming efficiency because of their wasted musculature, although can theoretically outswim anchovies (Wilson 1985b).

No reports have been documented at the breeding colonies to suggest that there are large numbers of penguins dying through starvation during the moult fast. Nor have there been many of reports of large numbers of dead penguins washing up along the coastline in a starved state, suggesting that most are dying at sea (Crawford *et al*. in press). One report was received on the 13 July of 2009 of 'hundreds of dead penguins' off Buffelsbaai (34°05'S, 22°59'E) off the Western Cape coast (D.M. Harebottle, Animal Demography Unit, University of Cape Town, 13 July 2009), although this could not be confirmed. During the pre-moult fattening, and the post-moult conditioning, the penguins are not constrained by breeding activities to return to the colony and are able to travel more widely to find food. Given the above factors, it is possible that the loss of penguins witnessed in the South African colonies is due to mortality after the moult fast, when the penguin is severely physiologically compromised, cannot swim fast due to loss of musculature, and succumbs to starvation, where the bodies are not found since they are further out to sea and get carried away by currents or sink.

Season and synchrony of moult

The seasonal trends for timing and synchrony of moult in adult plumaged African penguins reported for Namibia (Kemper 2006, Kemper *et al.* 2001, 2007, 2008) and in South Africa (Underhill and Crawford 1999, Crawford *et al.* 2006a, Wolfaardt *et al.* 2009) hold true for this study. In Namibia, African penguins in adult plumage were recorded moulting during each month of the year. At all localities, there was a minimum from July to September. Bimodal moult peaks are evident at all colonies with the exception of Possession Island (Kemper *et al.* 2008, this Chapter). The major peak occurred over April/May during autumn, with the minor peak occurring in December/January during summer conforming to the trend reported by Kemper *et al.* (2008). Moult seasonality was less clearly defined at Possession Island compared to the other three Namibian colonies, a similar finding to that of Kemper *et al.* (2008). The first peak of the year in December/January, which coincides with that of immature African penguins undergoing moult into adult plumage, is thought to be adult-plumaged African penguins younger than four years (Kemper and Roux 2005, Kemper *et al.* 2008). The second peak in April is considered to be made of breeding birds, i.e. birds older than six years. Similarly to what has been previously found, there was little difference in moult synchrony within the Namibian colonies (Kemper *et al.* 2008).

South African islands, showed a monomodal moult pattern, with peak moult occurring in summer from October to January, similar to that found in other studies (Randall and Randall 1981, Wilson 1985a, Underhill and Crawford 1999, Hemming 2001, Crawford *et al.* 2006a, Wolfaardt *et al.* 2009). At Dassen Island, although the moult period started earlier than at other Western Cape colonies, it is the least synchronous of all colonies. Breeding is recorded all year on Dassen Island, which may explain the less synchronous moult (Wolfaardt *et al.* 2009). The anchovy fishery is concentrated on the west coast of South Africa, close to Dassen Island (Crawford *et al.* 2006b). This suggests that there is an abundance of food for penguins in this area, allowing the breeding season to extend year round. Alternatively, it may indicate that the seasonality of moult has collapsed at Dassen Island where numbers have collapsed over the last 50–100 years. An

estimated 296 000 adult birds was recorded for Dassen Island in 1956 (Rand 1963a,b), compared to 10 276 in 2009. This could be a similar phenomenon to Possession Island where there are very few penguins now, compared to that of 50 years ago.

At Dyer Island, the peak moult was earlier and was the most synchronous of adult plumaged moulting birds. The high energy demands of moult have been considered to be incompatible with chick rearing (Payne 1972), and so is an activity that takes place outside of the breeding season (Boersma 1975, Randall and Randall 1981). It is a process reliant on food availability (Kemper *et al.* 2008), and it is this factor that may explain the synchrony of adult moult on Dyer Island. While penguins need to ensure that there is enough food brought to their chicks to enhance fledgling survival, they also need to ensure that there is enough food for them to fatten themselves sufficiently to get through moult (Davis and Renner 2003). If the availability of food is highly seasonal, as is the case in high latitude breeding locations (Davis and Renner 2003), and if adults are still provisioning for their chicks at the end of the breeding season, they need to make a decision at some point to abandon their chicks and look after their own survival (Moreno *et al*. 1997). In Namibia, a few cases of breeding during, or just before moult has been observed, including in a few banded individuals (Kemper *et al*. 2008), and there are instances of this occurring at Dyer Island, (V Strauss, L Waller pers obs). Since moulting adults are not able to feed, they need to survive off their fat reserves, and it is unlikely that any breeding attempts while undergoing moult were successful (Kemper *et al*. 2008). The survival of the moulting bird may become compromised if there is insufficient time to lay down enough fat reserves between its previous breeding attempt and forthcoming moult (Kemper et al. 2008). High synchronicity of adult moult on Dyer Island may explain why more numbers of orphan chicks are found at this island than at other colonies in South Africa toward the end of the breeding season when some adults abandon their nests in November to moult (Parsons and Underhill 2005, Underhill *et al.* 2006, Parsons *et al*. 2007). This has also been reported at Robben Island and Stony Point, but not in the numbers observed at Dyer Island. At St Croix, Randall and Randall (1981) found that adult penguins would delay moult until the chicks had fledged, suggesting that food may be more readily available.

Similar to the breeding patterns observed on Dassen Island, the Humboldt penguin *Spheniscus humboldti* in Chile and Peru also breeds throughout the year. It has peaks in egg-laying in April and August–September in Peru (Paredes *et al.* 2002) and May and October in Chile. These penguins are located along the coast of the Humboldt Upwelling and feed primarily on anchovy *Engraulis ringens* (Zavalaga and Paredes 1997). The catch per unit effort of this fish by the fishing industry is reported to be highest during summer (December–March) and lowest during winter (July–September) when the anchovy schools are more dispersed in deep water (Bakun 1987). Humboldt penguins moult during this time (February) as opposed to breeding, suggesting that recovery of condition (30% of initial weight loss) might be important for adult survival and a constraint on the timing of breeding (Paredes *et al.* 2002). This may explain the differences in synchrony observed at Dassen Island compared to Dyer Island. Off the west coast of South Africa, the presence of the anchovy fishery suggests a more readily available food source at a longer period during the year (Crawford *et al.* in press), than that which is potentially available to penguins on Dyer Island.

For all South African colonies, moult is more synchronous than breeding. The timing of moult has been thought to coincide with a predictable availability of food over the Agulhas Bank from September to February (Crawford *et al.* 2006a, Wolfaardt *et al.* 2008), when sardine and anchovy congregate there to spawn (Hampton 1987). For Dassen Island, approximately 200km from the Agulhas Bank, this food source would be available to moulting birds who are not constrained by feeding chicks (Wolfaardt *et al.* 2008). This may be the reason that more adult moulters than breeders are seen at Stony Point than the number of breeders indicate there would be for the year.

Evidence of shift in trends

The overall pattern, exhibited most clearly by Robben Island, was for the timing of moult to become less synchronized through time, with a tendency for the moult period to start about three weeks earlier, to reach its mid point about two weeks earlier, with little change in the timing of the endpoint of moult. Weimerskirch *et al.* (1992) found moult periods varied in emperor penguins *Aptenodytes patagonica*, which may have been in response to variation in food supply. Kemper *et al.* (2008) suggest a plasticity in the circannual moult cycle, where the

timing of moult in successive years appears to be flexible and state that the role of age and environmentally related variability versus individual variability in timing of moult needs further investigation. The differences in moult patterns between Namibia and South Africa, suggest that there is more plasticity in the Namibian moult cycles than there are in adult-plumaged moulters in South Africa. Kemper *et al*. (2008) found that the autumn moult was more synchronised than at any other time during the year however, mainly involving birds that were breeding in mid-summer and subsequently delayed moult. The colony moult synchrony cycles are different in South Africa, and the relationship to moult and breeding success patterns at each colony needs to be investigated further, since moult synchrony patterns may reflect breeding synchrony patterns (Kemper *et al*. 2008). A shift toward a trend in earlier moult at Robben Island may be due to a shift in the breeding cycle at Robben Island.

Concluding remarks

Serial moult counts conducted throughout the year are likely better than nest counts at estimating population size since peak breeding at a colony at a given year may be missed if the counts are done annually, and because the breeding may not be synchronised so that the peak is not representative of the true number of breeding pairs. Moult counts need to be done regionally however, since there is evidence of movement of birds between colonies during moult. A peak in moulting, especially at the South African colonies, indicates that a reasonable estimate of numbers can be obtained by counting during the main moult period only (Randall *et al.* 1986), reducing the number of counts required (Crawford and Boonstra 1994). This assumes the main moult period is known, and does not shift or is variable (Crawford and Boonstra 1994), and for some colonies this should be verified, e.g. at Stony Point.

Breeding activity, and thus the annual cycle is dictated by distribution, local climatic and oceanographic conditions, as well as abundance and distribution of food (Kemper *et al.* 2001). Moult and breeding success time series at colonies need to be continued, and the colony specific relationship between the timing of moult and breeding needs to be investigated, since this may give a clue as to the reason for observed shifts in moult seasonality.

The critical value of 12.7 days, used as to estimate the size of the moulting population, is based on a sample of 45 penguins, and has a standard deviation of 1.4 days, and was obtained at a single island from a sample of birds moulting at the same time (Randall and Randall 1981, Randall *et al*. 1986). Because so much hinges on this value it ought to be confirmed on a larger sample of birds, moulting at different colonies and at different stages in the moult period.
It is only for the African penguin that moult counts are used as a monitoring tool in the way described in this paper. Whether the approach used on the African penguin is feasible for other penguin species should be investigated.

At Dassen Island and Robben Island, counts were conducted along the coastline because this is where most penguins are considered to moult (Crawford and Boonstra 1994), although Wolfaardt *et al.* (2009) found substantial numbers of moulting penguins in the interior of Dassen Island. Where feasible, the number of birds that moult inland needs to be estimated at the bigger colonies such as Dassen Island and Robben Island, although the extent of the area that needs to be covered makes this difficult. Additionally, moult is an energy-demanding process (Hoye and Buttemer in press) that places a considerable amount of stress on penguins. Every effort needs to be made to reduce disturbance to moulting penguins during the moult count.

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Table 1: Colony, time series and source for adult-plumaged moulting African penguins in Namibia and South Africa, Figure 1 shows the location of colonies. (Data Source: MCM=Marine and Coastal Management, Department of Environmental Affairs, MFMR = Namibian Ministry of Fisheries and Marine Resources)

Breeding Colony	Location	Period	Source
Mercury Island	25°43'S 14°50'E	Nov 1989–Nov 2009	Kemper *et al.* 2001, 2008 MFMR unpubl. data
Ichaboe Island	26°17'S 14°56'E	May 1992–Sep 2009	Kemper *et al.* 2001, 2008 MFMR unpubl. data
Halifax Island	26°37'S 15°04'E	Aug 1989–Jan 2010	Kemper *et al.* 2001, 2008 MFMR unpubl. data
Possession Island	27°01'S 15°12'E	Jun 1996–Nov 2009	Kemper *et al.* 2001, 2008 MFMR unpubl. data
Dassen Island	33°25'S, 18°05'E	Nov 1994–Jun 2009	Wolfaardt *et al.* 2009, CapeNature unpubl data
Boulders	34°11'S, 18°27'E	Jul 1992–May 2001	MCM and South African National Parks unpubl. data
Robben Island	33°48'S, 18°22'E	Oct 1988–June 2009	Underhill and Crawford 1999, Wolfaardt *et al.* 2009, DEA unpubl. data
Stony Point	34°22'S, 18°54'E	Oct 2000–Feb 2001	Hemming 2001
		Oct 2010–Feb 2011	CapeNature/Overstrand Municipality unpublished data
Dyer Island	34°41'S, 19°25'E	Sep 1999–Jun 2010	CapeNature unpubl data
St Croix Island	33°48'S, 25°46'E	Jul 1979–Jun 1981	Randall 1983, Randall *et al.* 1986 MCM unpubl. Data
Bird Island	33°50'S, 26°17'E	Jun 1992–Jun 1997	Randall 1983. MCM unpubl.data data

Table 2: The estimated number of African penguins in adult plumage at Mercury Island, Ichaboe Island, Halifax Island and Possession Island in Namibia, the maximum count of active nests and the relationship between adult plumaged moulters and breeding adults (2×active nests – see text) and active nests.

	Mercury Island			Ichaboe Island			Halifax Island			Possession Island		
Year	No.of adult moulters	No. of breeding birds	Ratio: moulters: breeding adults	No.of adult moulters	No. of breeding birds	Ratio: moulters: breeding adults	No.of adult moulters	No. of breeding birds	Ratio: moulters: breeding adults	No.of adult moulters	No. of Breeding birds	Ratio: moulters: breeding birds
1991	10189	7128	1.43	–	4355	–	–	1740	–	–	1371	–
1992	12209	7152	1.71	9226	4836	1.91	–	1380	–	–	1338	–
1993	11415	7332	1.56	9428	5310	1.78	–	1418	–	–	1502	–
1994	12610	4244	2.97	9185	5472	1.68	–	1362	–	–	1012	–
1995	16765	4522	3.71	9643	6686	1.44	1359	946	1.44	–	1216	–
1996	17678	4774	3.70	8079	5280	1.53	2186	768	2.85	2411	996	2.42
1997	15703	5324	2.95	6811	3806	1.79	2226	862	2.58	2253	1024	2.20
1998	16456	5768	2.85	6580	3124	2.11	1648	888	1.86	1944	930	2.09
1999	16104	6082	2.65	6422	3462	1.85	2482	994	2.50	1872	954	1.96
2000	15270	5644	2.71	6429	2690	2.39	3246	740	4.39	1307	718	1.82
2001	14254	5230	2.73	7104	4520	1.57	3403	1040	3.27	1343	724	1.86
2002	13679	6924	1.98	6772	4364	1.55	3544	1016	3.49	1519	812	1.87
2003	12544	5566	2.25	6154	4316	1.43	3404	1068	3.19	1259	744	1.69
2004	11718	4074	2.88	6048	1728	3.50	3767	1338	2.82	1396	890	1.57
2005	11109	4910	2.26	6083	2154	2.82	–	1224	–	1537	940	1.64
2006	12343	3626	3.40	4627	1430	3.24	–	610	–	1661	712	2.33
2007	12068	–	–	3425	–	–	4104	–	–	1894	–	–
2008	–	–	–	3195	–	–	5182	–	–	–	–	–
n			16			15			10			11
Mean			2.61			2.04			2.84			1.95
SD			0.7022			0.6584			0.8328			0.2818

Table 3: The estimated number of African penguins in adult plumage at Dassen Island, Robben Island, Boulders, Stony Point, Dyer Island and Bird Island, the maximum count of active nests and the relationship between adult plumaged moulters and breeding adults (active nests x2) and active nests.

	Dassen Island			Robben Island			Boulders			Stony Point			Dyer Island		St Croix	Bird Island		
Year	No.of adult moulters	No. breeding adults	Ratio: moulters: breeding adults	No.of adult moulters	No. breeding adults	Ratio: moulters: breeding adults	No.of adult moulters	No. breeding adults	Ratio: moulters: breeding adults	No.of adult moulters	No. breeding adults	Ratio: moulters: breeding adults	No.of adult moulters	No. breeding adults	Ratio: moulters: breeding adults	No. breeding adults	No.of adult moulters	No. breeding adults	Ratio: moulters: breeding adults
1988	–	13016	–	3457	1698	2.04	–	68	–	–	110	–	–	26830	–	38919	–	6014	–
1989	–	16856	–	3392	1658	2.05	–	76	–	–	138	–	–	21764	–	38926	–	6710	–
1990	–	17440	–	4730	2556	1.85	–	108	–	–	178	–	–	16698	–	38934	–	7406	–
1991	–	18024	–	4915	3758	1.31	–	262	–	–	154	–	–	12230	–	38941	–	6388	–
1992	–	15126	–	6538	4054	1.61	–	316	–	–	114	–	–	15158	–	38949	–	7568	–
1993	–	14398	–	8002	4352	1.84	564	482	1.17	–	80	–	–	4748	–	38956	8707	4586	1.90
1994	12360	18778	0.66	7948	5598	1.42	801	718	1.12	–	88	–	–	9298	–	37125	5656	5944	0.95
1995	12222	19584	0.62	6563	4558	1.44	1369	732	1.87	–	102	–	–	8520	–	35302	8512	7302	1.17
1996	12953	19004	0.68	5608	6194	0.91	885	832	1.06	–	116	–	–	6558	–	33479	7421	5272	1.41
1997	16296	17302	0.94	8696	6672	1.30	1031	1452	0.71	–	130	–	–	5490	–	31656	9299	3242	2.87
1998	21438	21836	0.98	9397	6934	1.36	2352	1110	2.12	–	144	–	8415	3926	2.14	29833	–	5504	–
1999	25074	30310	0.83	11765	8798	1.34	2030	1812	1.12	–	176	–	4564	4726	0.97	28010	–	7766	–
2000	26095	31196	0.84	13362	11410	1.17	3664	1898	1.93	4545	208	21.85	4717	4440	1.06	30422	–	8186	–
2001	25619	42818	0.60	16439	13446	1.22	–	2108	–	–	222	–	4216	4176	1.01	33900	–	10752	–
2002	22511	45766	0.49	14737	14504	1.02	–	2166	–	–	234	–	5052	4290	1.18	26066	–	6312	–
2003	17592	40638	0.43	17424	12866	1.35	–	2066	–	–	246	–	6177	3858	1.60	18232	–	1872	–
2004	18298	49802	0.37	12871	17048	0.75	–	2392	–	–	196	–	3414	4432	0.77	20176	–	5902	–
2005	11350	45374	0.25	7768	14304	0.54	–	2454	–	–	372	–	3348	4106	0.82	8306	–	6406	–
2006	7876	26566	0.30	6496	7394	0.88	–	2150	–	–	530	–	2973	4114	0.72	16154	–	5644	–
2007	2312	23570	0.10	5197	11870	0.44	–	1648	–	–	520	–	2807	3026	0.93	8726	–	2806	–
2008	442	11438	0.04	3589	4468	0.80	–	1826	–	–	620	–	2420	3210	0.75	15478	–	5530	–
2009	–	10276	–	3956	4830	0.82	–	1408	–	4365	974	4.48	3133	2520	1.31	13648	–	5248	–
2010	–	9858	–	–	–	–	–	1866	–	4701	932	5.04	–	–	–	–	–	–	–
		N	15		N	22		n	8					n	12			n	5
		Mean	0.54		Mean	1.25		Mean	1.39					Mean	1.10			Mean	1.66
		SD	0.2934		SD	0.4525		SD	0.5097					SD	0.4129			SD	0.7626

Table 4: Peak adult moult summary for Mercury Island (1991–2009), Ichaboe Island (1992–2009), Halifax Island (1995–2009) Possession Island (1996–2009), Dassen Island (1994–2009), Robben Island (1998–2009), Boulders (1992–2001), Dyer Island (1998–2009) and Bird Island (1992–1997.

Island	Peak % moulting	Week of peak moult	Week date of peak moult	Cumulative % birds moulted by date of peak moult	% moulted in 6 week period around peak moult	Six-week period during peak moult
Mercury Island	6.1	35	26 Apr–2 May	71.8	32.9	32–37
Ichaboe Island	4.5	35	26 Apr–2 May	70.5	24.1	35–40
Halifax Island	4.1	34	19–25 Apr	76.3	21.9	33–38
Possession Island	3.1	35	26 Apr–2 May	70.3	17.4	33-38
Dassen Island	6.5	21	18–24 Nov	40.8	39.4	19–24
Robben Island	9.9	23	2–8 Dec	52.5	50.9	20–25
Boulders	11.8	21	18–24 Nov	38.6	59.6	19–24
Dyer Island	15.1	19	4–10 Nov	54.8	67.1	16–21
Bird Island	6.6	23	3–8 Dec	48.0	37.5	19–26

Table 5: Synchronisation of moult of African penguins. The week in which 50% of African penguins had moulted and the period in weeks in which 60% of adult African penguins had been recorded moulting at Mercury Island (1991–2009), Ichaboe Island (1992–2009), Halifax Island (1995–2009), Possession Island (1996–2009) in Namibia, and Dassen Island (1994–2009), Robben Island (1988–2009) and Dyer Island (1998–2009) in South Africa. The SD of the week in which 50% of the penguins had moulted measures the extent of inter-year variability in the timing of moult. The mean of the period in which 60% of the penguins had moulted measures the synchronization of moult at that colony and the SD measures the extent of variability of this measure.

Island	n	Week by which 50% of penguins had moulted		Duration of period in which 60% of penguins had moulted	
		Mean	SD	Mean	SD
Mercury Island	17	31.5	1.9	20.7	5.6
Ichaboe Island	17	28.8	4.2	21.4	4.0
Halifax Island	12	25.6	3.1	21.1	2.8
Possession Island	13	27.9	6.4	24.2	6.2
Dassen Island	14	22.7	1.5	10.4	1.7
Robben Island	21	23.0	1.2	7.5	1.8
Dyer Island	11	18.8	0.6	5.5	0.9

Table 6: Regression model results to test if moult was starting earlier in each year. Year was set as explanatory variable. The 20, 50, 80 % columns indicate cumulative percentage moult. Negative values in these columns indicate moult is getting earlier. Time series for Mercury Island (1991/92–2007/08), Ichaboe Island (1992/93–2008/09), Halifax Island (1995/96–2008/09), Possession Island (1996/97–2008/09) in Namibia and Dassen Island (1994/95–2007/08), Robben Island (1988/89–2008/09), Boulders (1993/94–200/01) and Dyer Island (1998/99–2008/09) in South Africa.

Colony	Duration (weeks)	20%	50%	80%
Mercury Island	0.471	0.066	–0.101	–0.154
Ichaboe Island	–0.225	–0.005	–0.159	–0.230
Halifax Island	0.391	–0.434	–0.595	–0.043
Possession Island	–1.038	0.297	0.022	–0.742
Dassen Island	0.154	–0.310	–0.22	–0.156
Robben Island	0.135	–0.179	–0.081	–0.044
Boulders	0.298	–0.500	–0.512	–0.202
Dyer Island	0.036	–0.009	0.018	0.027

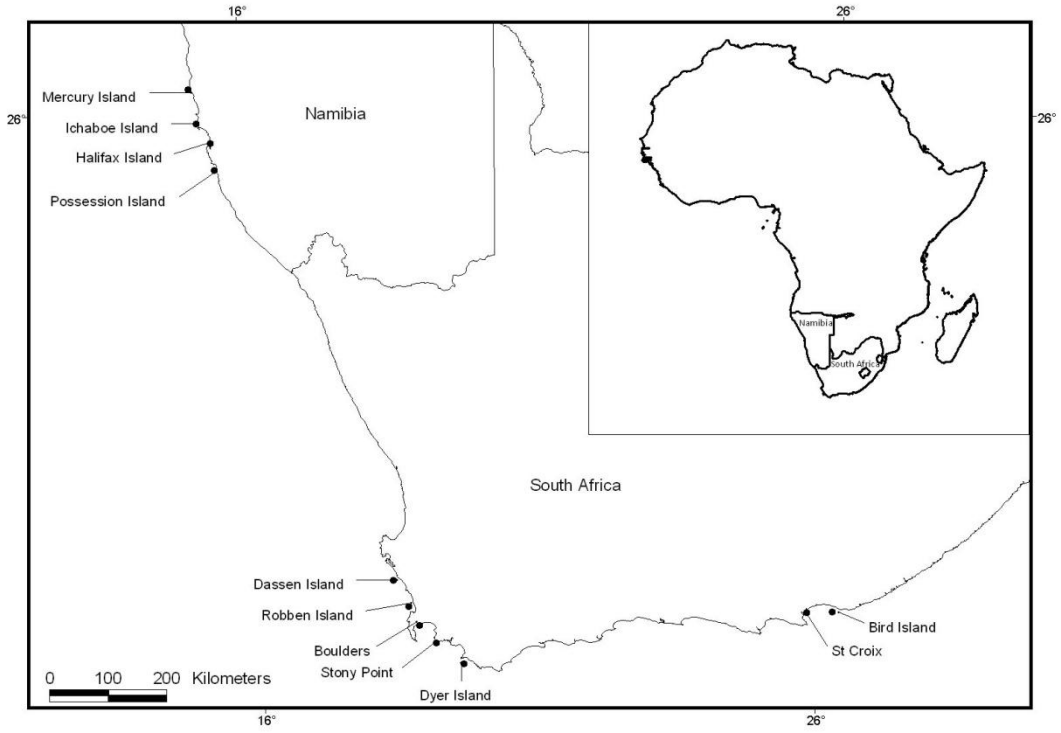

Figure 1: Map of Namibia and South Africa, showing the African penguin breeding colonies mentioned in the text

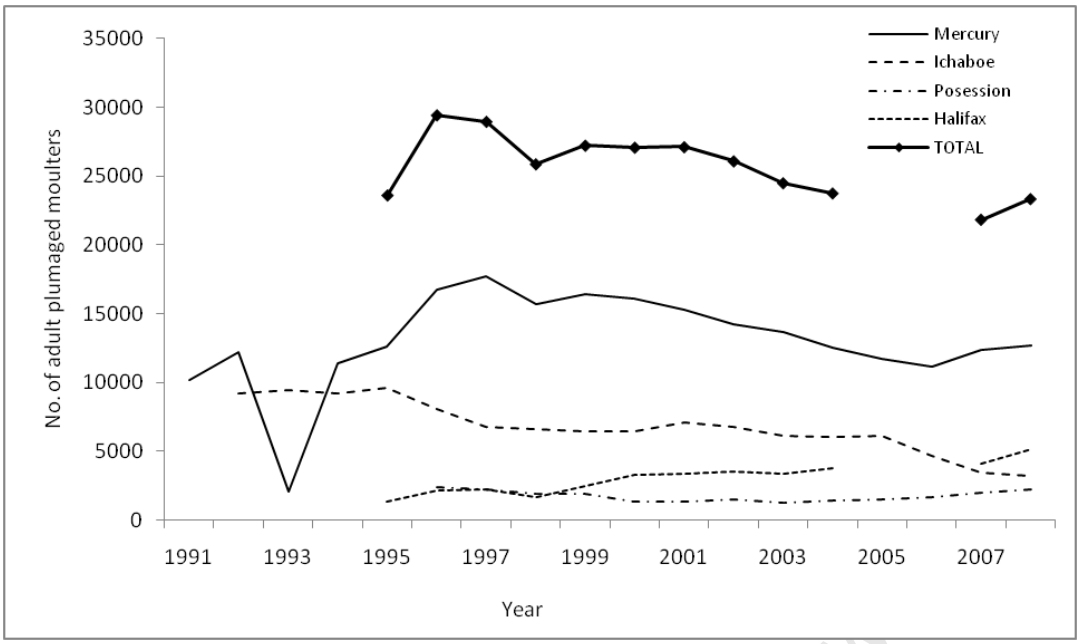

Figure 2: Population trends of African penguins in adult plumage based on serial counts of moulting individuals at Mercury Island, Ichaboe Island, Halifax Island, Possession Island in Namibia. The 'Total' line displays trends only for years in which data was available for all colonies

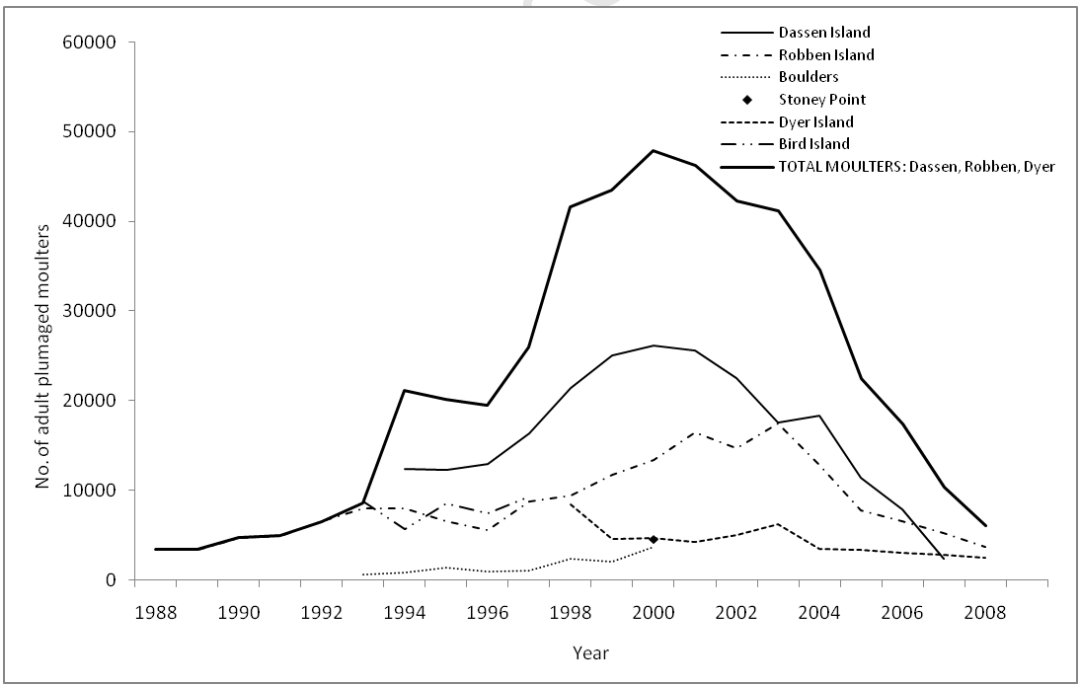

Figure 3: Population trends of African penguins in adult plumage, based on serial counts of moulting individuals Dassen Island, Robben Island, Boulders, Dyer Island, and Bird Island. A total is included for Dassen Island, Robben Island and Dyer Island

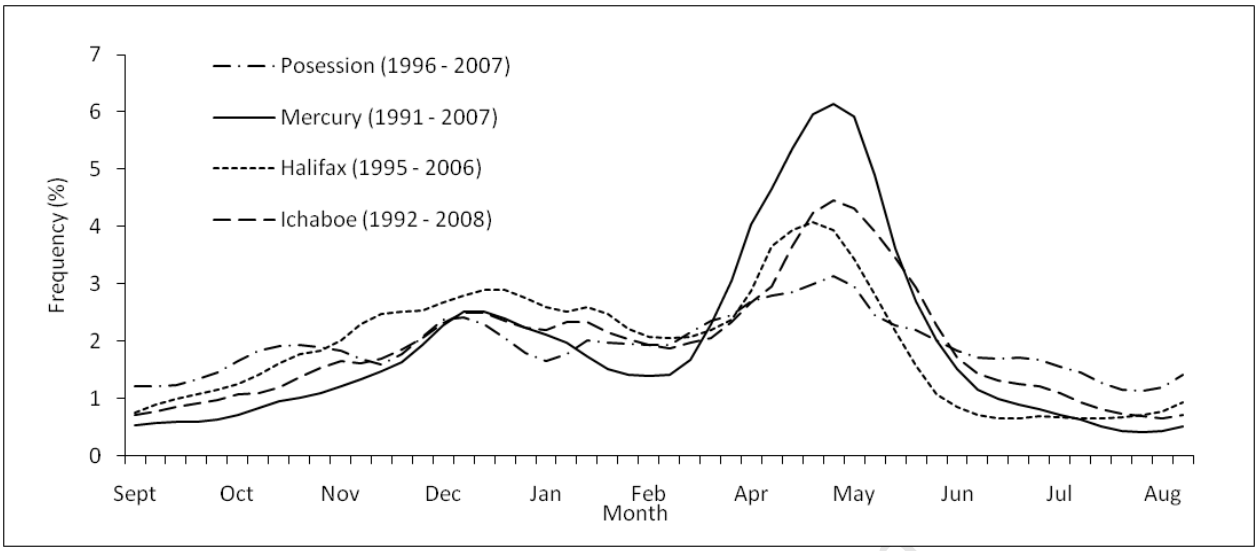

Figure 4: Average seasonal pattern of moult for adult-plumaged African penguins at Mercury Island (1991–2007), Ichaboe Island (1992–2008), Halifax Island (1995–2006) and Possession Island (1996–2007), expressed as a proportion of birds moulting in each week.

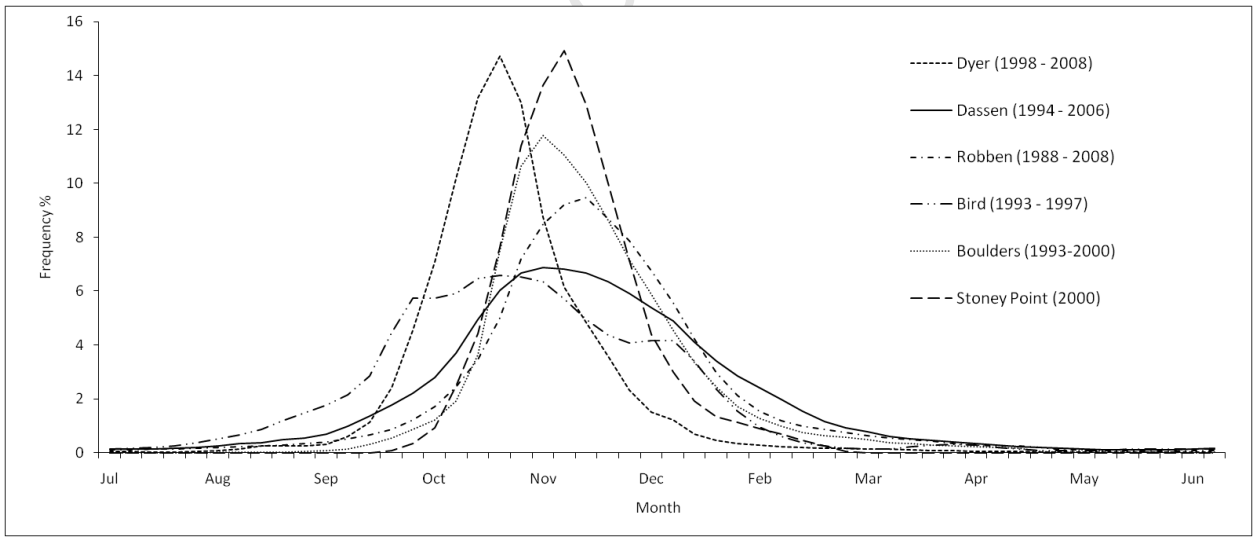

Figure 5: Average seasonal pattern of moult for adult plumaged African penguins at Dassen Island (1994/95–2005/06), Robben Island (1988/89–2005/06), Boulders, Stony Point (2000/2001), Dyer Island (1997–2008), and Bird Island (1993–1997), expressed as a proportion of birds moulting in each week.

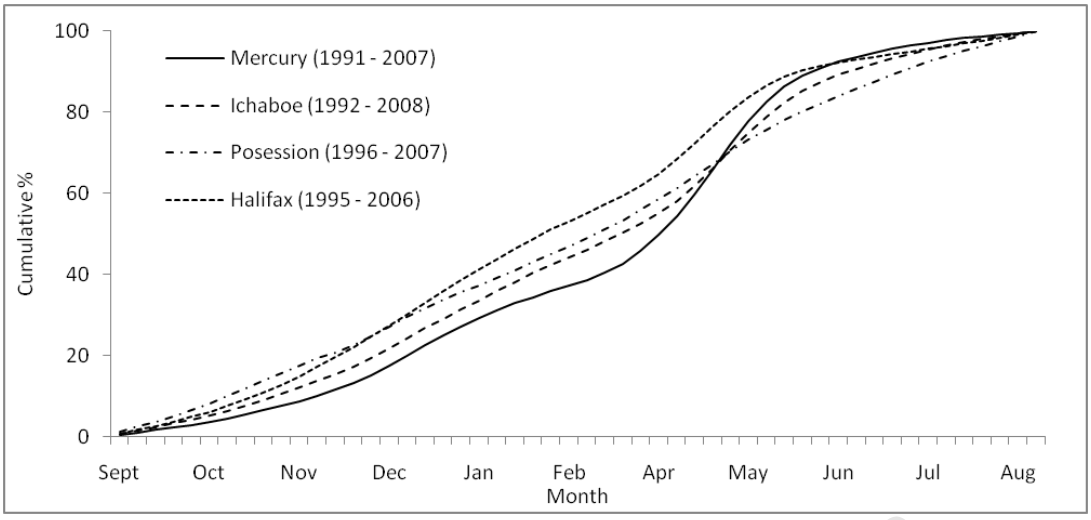

Figure 6: Average cumulative pattern of moulting adult plumaged African penguins at Mercury Island, Ichaboe Island, Halifax Island and Possession Island expressed as a cumulative proportion of birds moulting in each week. Week 1 is the week beginning 1 September

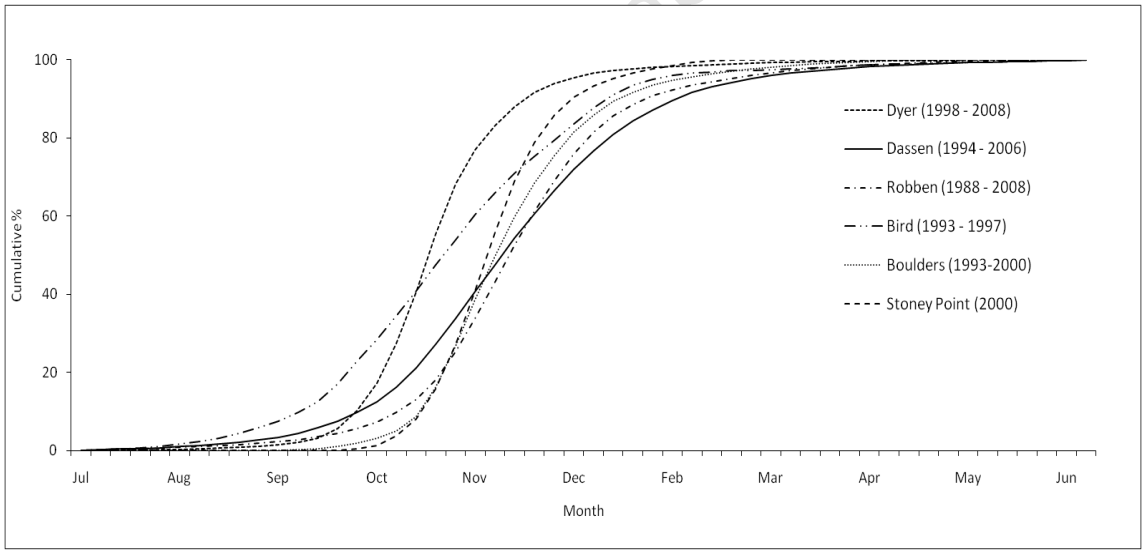

Figure 7: Average cumulative pattern of moulting adult plumaged African penguins at Dassen Island, Robben Island, Boulders, Stony Point, Dyer Island, St Croix and Bird Island expressed as a cumulative proportion of birds moulting in each week. Week 1 is the week beginning 1 July

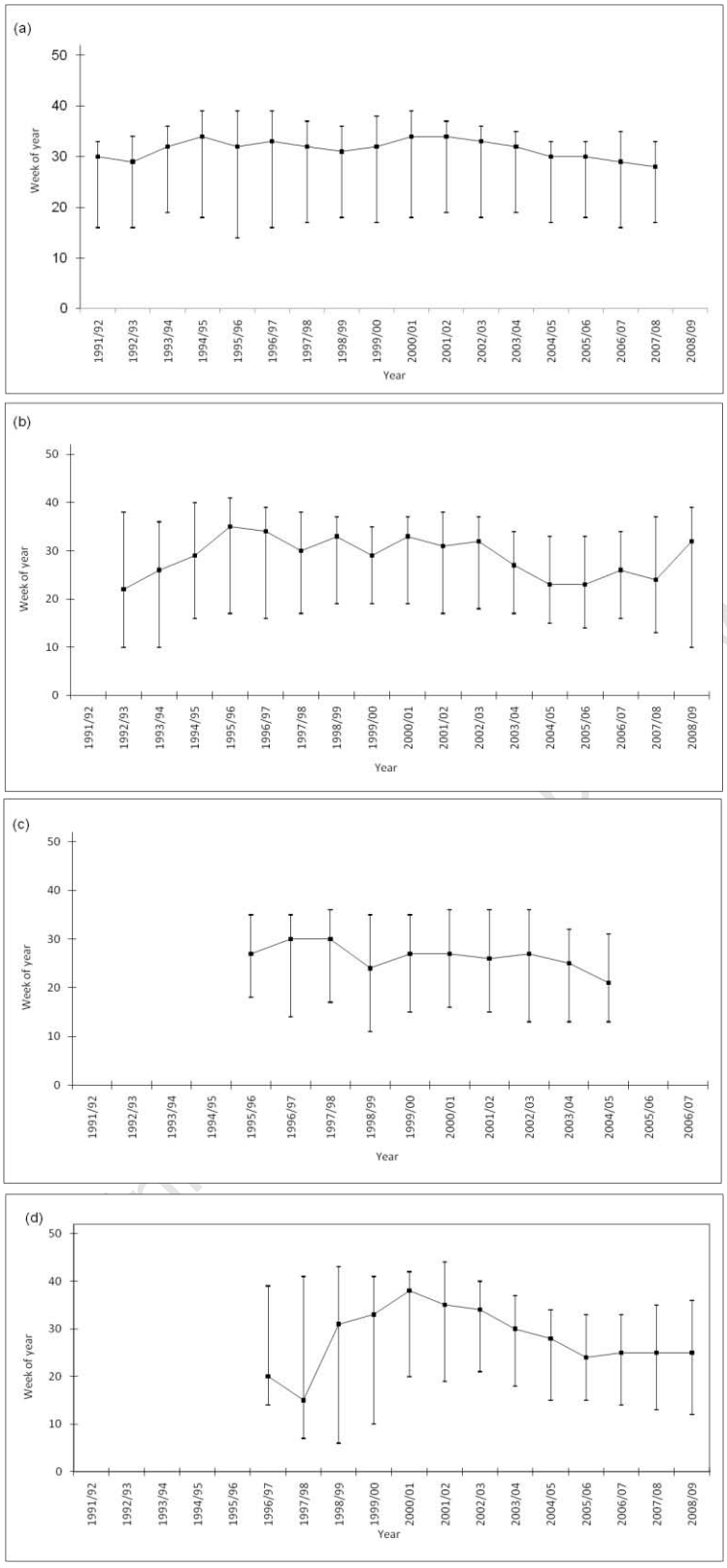

Figure 8: Cumulative percentages of adult African penguins moulting per week at a) Mercury Island, b) Ichaboe Island, c) Halifax Island, d) Possession Island in Namibia. The week in which 50% of birds had been recorded moulting is represented by the joined squares. The lower and upper error bars represent weeks in which 20% and 80% of birds had been recorded moulting respectively. The year starts on 1 September for Namibian colonies

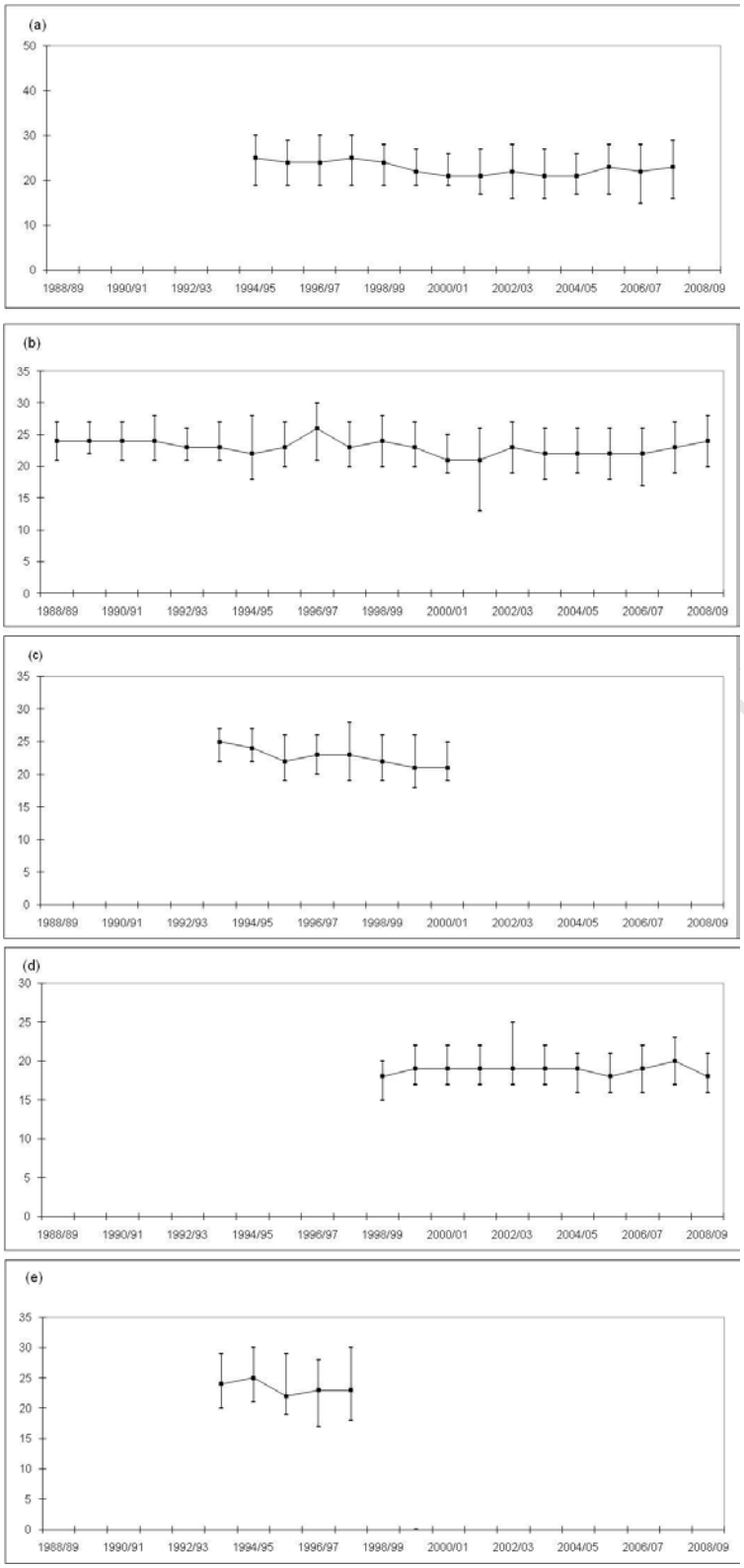

Figure 9: Cumulative percentages of adult African penguins moulting per week at (a) Dassen Island (b) Robben Island (c) Boulders (d) Dyer Island (e) Bird Island. The week in which 50% of the birds had been recorded moulting is represented by the joined squares. The lower and upper error bars represent the weeks in which 20% and 80% of birds had been recorded moulting respectively. The year starts on 1 July for South African colonies

CHAPTER 4

CHICK CONDITION IN AFRICAN PENGUINS

Photo: D Geldenhuys

CHICK CONDITION OF AFRICAN PENGUINS

ABSTRACT

As central place foragers, breeding African penguins *Spheniscus demersus* are sensitive to local food availability. Chick body condition can therefore be used as an indicator of local feeding conditions. African penguin chick condition was measured at a target sampling interval of five to ten days at five South African colonies between 2008 and 2009. A condition index, based on maximal growth relative to structural size and using quantile regression techniques, was used to compare chick condition between colonies, years and seasons. Data collected for African penguins at Robben Island in 2004, a year of below average breeding success, provided the baseline reference point. Overall for all colonies studied, chick condition was poorer in 2008 (0.3580) than that on Robben Island in 2004 (0.5367). Overall chick condition in 2009 (0.2846) was significantly poorer than that in 2008. Dyer Island was the colony with the consistently poorest chick condition (0.2800 and 0.2066 in 2008 and 2009 respectively). In light of an experimental fishing closure experiment that involved four of the South African colonies, the condition index was shown to be a useful tool to compare the body condition of a group of chicks of various sizes and of unknown age between breeding colonies. The condition index should preferably be interpreted together with other seabird demographic and foraging information in terms of local conditions.

KEY WORDS

African penguin, Benguela Upwelling Ecosystem, chick condition, food variability

INTRODUCTION

Marine top predators, such as African penguins *Spheniscus demersus,* provide insights into regional ocean productivity and the rate and nature of ecosystem changes (Bradshaw *et al.* 2000, Boersma 2008). The African penguin is a southern African endemic, which breeds within the Benguela Upwelling Ecosystem (Crawford *et al.* 2006b), an ecosystem characterised by high, but spatially and temporally highly variable, productivity (Crawford 1999, Field and Shillington 2004, van der Lingen *et al.* 2006, Hutchings *et al.* 2009). Within the southern Benguela Upwelling Ecosystem,

African penguins feed primarily on sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* (Rand 1960, Crawford *et al*. 2010) and as pelagic 'samplers' they are sensitive to their environment, responding quickly to environmental changes (Boersma 2008). Their breeding success and regional population trends in South Africa for example, have been related to changes in the abundance and distribution of the pelagic sardine and anchovy within their breeding grounds (Crawford 1998, Crawford *et al.* 2001, 2006a, 2008a, b, Underhill *et al.* 2006).

Reproductive performance of seabirds can be used as indicators of food availability (Cairns 1987, Williams and Croxall 1990, Boersma 2008). Adult penguins are central place foragers when breeding, returning regularly to the colony to provision their chicks and are thus range-restricted during the breeding season (Clarke 2001, Crawford *et al.* 2006a, Boersma 2008). African penguin chicks are altricial, dependant on their parents to provision food for them, and so studies of chick condition are an indicator of feeding conditions around the breeding colony (Williams and Croxall 1990, Bradshaw *et al.* 2000).

A mismatch between prey distribution and seabird breeding colony locations has recently occurred in South Africa (Crawford *et al*. 2007), causing declines in several southern African endemic seabird species including the African penguin (Crawford *et al.* 2007, Durant *et al*. 2010, Pichegru *et al*. 2009, 2010). It is thought that the combination of fishing pressure (Coetzee *et al.* 2008) and changes in the marine environment (Roy *et al.* 2007) in the southern Benguela Upwelling Ecosystem have resulted in the eastward shift in sardine and anchovy (Fairweather *et al.* 2006, Crawford *et al*. 2007), displacing the stocks outside the foraging range of breeding penguins (Crawford *et al.* 2006a, 2008a, b) and causing these seabird population declines. Mullers *et al.* (2009) showed that growth of chicks of species that use the same resources as purse-seiners are likely to respond to changing in availability of sardine and anchovy, which is similar to findings of Hennicke and Culik (2005) who found that patterns of growth in Humboldt penguins *S. humboldti* reflected local food availability. Additionally, Boersma *et al.* (2009) found in their study that when penguins fed close to the colony they reared more chicks than at colonies where they travelled further to find food.

Given the African penguin population decline, that this population trend is associated with distribution and abundance of fish stocks, as well as the ability to use African

penguins as indicators of fish availability, the then South African Department of Environmental Affairs and Tourism initiated a two year feasibility study in 2008 which aimed to investigate the impact of fishing closures around certain African breeding colonies on penguin breeding success. Five coastal island breeding colonies of South Africa were involved in this experiment. During 2008 and 2009, the area within a 20km radius of Dassen Island was closed to fishing, while the areas around Robben and Dyer Islands remained open. The areas around St Croix and Bird Islands were open to fishing in 2008, and an area around St Croix was closed to fishing in 2009 (Island Closure Task Team 2010).

In order to assess the impact of these closures and whether the establishment fishing closures around the colonies would improve breeding success, several parameters of African penguins influenced by food supply were monitored, including numbers of breeding pairs, number of moulters, foraging behaviour, diet, chick growth and condition (Island Closure Task Team 2010). This chapter discusses findings on African penguin chick condition.

Body condition of an animal refers to the proportion of its body mass which is available to it in the form of metabolizable energy reserves (Lubbe 2008) and is an estimate of an animal's nutritional state (Jakob *et al.* 1996). A condition index determines the mass of the individual associated with energy reserves, after correcting for body size, when comparing body mass or other measures of nutritional state across individuals (Jakob *et al.* 1996, Green 2001, Schulte-Hostedde *et al.* 2005). The condition of a chick is dependent on the parent's ability to provision the chick (Lubbe 2008), and is thus a useful indicator as to the local availability of food to the provisioning parent.

Lubbe (2008) developed a chick condition index that can be used for African penguin chicks. The index is based on the relationship between chick body mass and total head length (see Methods below). The aims of this chapter are to explore the application of this condition index; variability of the chick condition index within breeding years, between breeding years and between colonies. I also looked at the variability of chick condition in relation to hatching order. The condition index is discussed in light of potential impacts of fishing closures. Guidelines for the frequency of data collection are also considered.

METHODS

Data collection

During 2008 and 2009, chick condition data were collected at Dassen Island (33°25' S, 18°06'E), Robben Island (33°48' S, 18°22'E), Dyer Island (34°41' S, 19°25'E), St Croix Island (33°44' S, 25°46'E) and Bird Island (33°50' S, 26°17'E) in South Africa (Figure 1) as part of the 'Island Closure Feasibility Study', co-ordinated by the (then) Marine and Coastal Management department (MCM), a sub-directorate of the Department of Environmental Affairs. Data from Dassen Island were collected by staff from CapeNature and MCM, on Dyer Island by the author and CapeNature staff, on Robben Island by Dr R Sherley (University of Bristol) and Dr N Parsons (MCM), and on Bird and St Croix Islands by Dr L Pichegru and her students from the University of Cape Town as well as by staff from South African National Parks. Data from Halifax (26°39'S, 15°04'E) and Mercury Islands (25°43'S, 14°50'E) in Namibia were obtained from Dr K Ludynia and Dr J Kemper of the University of Cape Town and the Ministry of Fisheries and Marine Resources, Namibia (Figure 1). Data collected from Robben Island in 2004 were collected by S. Bouwhuis as part of a study on the prefledging energetics of African penguins (Bouwhuis *et al.* 2007).

For all colonies and years, total head length (from the tip of the culmen to the base of the skull) was measured to the nearest 0.1mm with vernier callipers. Chicks with total head lengths of <75mm were not measured following Lubbe (2008). Lubbe (2008) found the period of linear growth between head length and mass corresponded with chicks older than 20 days, the growth in chicks younger than 20 days is slow (Cooper 1977) and thus differences in body condition were considered negligible at that early stage (Lubbe 2008). Chicks with head lengths less than 75mm were thus not weighed and included in the condition analyses. Furthermore, by weighing older chicks, the risk of disturbance to the nest in the early chick rearing period was also reduced (Hockey and Hallinan 1981), an important consideration in a rapidly declining (Underhill *et al.* 2006), then 'Vulnerable,' now 'Endangered' species (BirdLife International 2010). Date of hatching and hatching order was thus not known, and the hatching order of two chick broods was determined by size differences on the first nest visit. The first hatching chick was designated the (A-chick), second hatching chick (B-chick) and if only one chick was present, it was designated a singleton. Chicks were subsequently marked with

Porcimark®, an animal marker dye, in order to follow the same chicks throughout the season.

Body mass was measured to the nearest 10g using hand-held electronic balances (on Dassen, Robben and Dyer Islands) and Pesola® spring balances (on Mercury, Halifax, St Croix and Bird Islands). Chicks were weighed in a bag or in a harness. The date of each measurement was recorded, and all chicks were measured between 8:00 and 17:00 to minimise disturbance to feeding parents and the possible distortion of mass measurements being influenced by feeding events.

In South Africa, samples of chicks were measured at a target interval of five to 10 days. This was not always achieved as a result of colony access being hindered by weather and sea conditions (Table 1 provides average intervals). In Namibia, chicks were weighed at irregular, opportunistic, intervals. Sample sizes, dates and nest visit intervals are summarised in Table 1.

Body condition index

Lubbe's (2008) condition index is based on concepts developed by Veen *et al.* (2003) for measuring the condition of tern chicks in West Africa. Lubbe's (2008) aim was to develop an index that was independent of the size of the chick and to find a non-invasive and rapid sampling protocol that provides a snap-shot of the relative condition of African penguin chicks of varying sizes and unknown ages within a colony on a single sampling visit, so as to enable comparison the average body condition between colonies (Lubbe 2008). Lubbe's (2008) index is a relative, rather than absolute measure, of condition, in that it uses the condition of penguin chicks successfully surviving to fledging on Robben Island in 2004 as the baseline (see Methods and Discussion below).

Veen *et al.* (2003) calculated body condition using a curve, fitted by eye, to represent the maximal mass of chicks relative to a structural measure (total head length). For the original Veen index, condition of the individual chicks was calculated as:

Veen's condition index = observed mass/maximum mass at given body size.

The condition index developed by Veen et al. (2003) is the fraction of maximum mass achieved by a chick with a given body size. Lubbe (2008) modified this index by using

quantile regression techniques (Koenker and Bassett 1978) instead of subjectively fitting the curve by eye and by adding lower and upper "growth lines", i.e. the 5% and 95% quantile regression lines, with total head length as explanatory variable and mass as the response variable. Lubbe (2008) defined the condition of individual chicks as the proportion of the distance between the upper and lower quantiles for a chick with a particular total head length. It was calculated as

Lubbe's condition index = (observed mass – predicted 5% mass) /
(predicted 95% mass – predicted 5% mass),

where the predicted 5% mass and the predicted 95% mass for a given total head length were calculated from the 5% and 95% quantile regression lines derived from a data set of (1168 measurements on) 125 chicks which fledged successfully on Robben Island in 2004 (Bouwhuis *et al.* 2007, Lubbe 2008, S Bouwhuis *in litt.*). The body condition index is scaled in such a way that a value of 1.0 indicates condition at the 95% percentile, 0.0 indicates condition at the 5% percentile, so that a condition index value of 0.5 represents the average condition of chicks on Robben Island in 2004. Values for the body condition index exceeding 1.0 and values below 0.0 are valid. The condition index is not measured on a ratio scale for which the zero value is absolute; the concept of the coefficient of variation of the condition index is therefore undefined (Underhill 1999).

For the sample of data collected on Robben Island in 2004, Lubbe (2008) found that the relationship between mass and total head length was almost linear once the total head length exceeded 75mm. Chicks with total head length less than 75mm were therefore excluded from the calculations. I checked whether the linear relationship found by Lubbe (2008) was upheld by using a larger sample of measurements from six breeding colonies over multiple years. Lubbe (2008) also found that the relationship between mass and other easily measurable parts of the body, for example, flipper length and tarsus length, did not show a linear relationship with mass, and were less suitable for the construction of an easily interpretable condition index.

Data analysis

Effectiveness of the condition index in compensating for size

To be valid, the condition index needs to be independent of the size of the chicks. This was assessed by performing a correlation analysis between the condition index and head

length, using the entire data set and a subset comprising data collected during the peak of the chick-rearing period, April–September, which was also the period for which most observations were available.

Relationship between condition index and explanatory variables

The objective of the statistical analyses was to investigate how Lubbe's (2008) chick condition index varied spatially and temporally. I also explored the extent to which condition varied depending on hatching order.

The condition indices were modelled in relation to explanatory variables using multiple linear regression analyses. Explanatory variables used in the models were year (2004, 2008, 2009), colony (Mercury, Halifax, Dassen, Robben, Dyer, St Croix, Bird) colony-year (colony at a specific year), month and hatching order. I also tested whether the condition index showed autocorrelation through time within years. Calculations were performed using GENSTAT 13.1 (Payne *et al*. 2010).

I assessed the overall annual pattern of the condition index, by pooling all available data for South Africa for 2004, 2008 and 2009. To examine the seasonal pattern, a regression model was fitted with month as a factor variable. In order to assess the inter-colony and monthly variation, the variability in the monthly mean condition was plotted for each month that data were available for each colony. Differences in chick condition between 2008 and 2009 were assessed by fitting a model with parameters for each of the two years and for each colony using Robben Island as the reference colony and 2004 as the reference year.

For broods of two chicks, I predicted that the condition of the A-chick would, on average be better than that of the B-chick, and anticipated that the condition of single chick broods would be comparable or better than that of the A-chick in a two-chick brood. Data on chick status were available for Dyer Island in 2008 and 2009, and for a subset of the chicks measured on Dassen Island and Robben Island in 2009.

Relationship between average condition and variability in condition

I hypothesized that when feeding conditions were good, all parents would find adequate food, and most chicks would be in a uniformly good condition and would show relatively little variability. In contrast, when feeding conditions were poor, the chicks of the best

quality parents would be in good condition, while those of poor quality parents would be in poor condition, and the variability of chick condition would be large. In order to test this prediction, I related the variability of the condition index to the condition index itself. I calculated the mean condition index and the standard deviation of the condition index for sampling days on which 10 or more chicks were measured. I tested for a negative correlation between the standard deviation of condition and the mean condition on these days.

Sampling frequency recommendations

In order to make recommendations for effective future chick condition sampling protocol, datasets from colonies with large numbers of observations in a single year were selected. These datasets were successively pooled to examine the changes which sampling frequency would make to the percentage variability explained in the model. Datasets were analysed both over the whole year, and for the period April–September, the peak chick-rearing period at colonies in South Africa, and therefore the time during which most observations were made.

RESULTS

A total of 7287 measurements of body mass and head-length were available for the analyses (Table 1). Data were collected from February to November at five African penguin breeding colonies in South Africa. The largest data sets were for Robben Island 2004 (n=1168), 2008 (n=762), 2009 (n=1176), Dassen Island 2009 (n=947), Dyer Island 2008 (n=978) and 2009 (n=883). For the period April–September, the period of the breeding season when most chicks are present (Randall 1983, Crawford *et al*. 1999), for 2004, 2008 and 2009, the total number of South African chick condition observations was 5971 (Tables 2 & 3). Data from the Namibian colonies were collected in February, March, April. August, September and October.

The average number of measurements for each colony taken on one day ranged from six at Halifax Island in 2009 to 41 on St Croix Island in 2009, with a mean of 22 samples per sampling date (Table 1). The largest gaps between sampling dates in a breeding season were 170 days at Halifax Island and 167 days at Mercury Island, both in 2009, and 104 days at St Croix Island in 2008 and 92 days at Bird Island, in 2008 (Table 1).

Effectiveness of the condition index in compensating for size

The condition index removed the effect of the size of the bird. For the entire data set (n=7287) the correlation between head length and the condition index was 0.056, indicating that head length accounted for only 0.32% of the variability in condition. For the sample of 5971 chicks between April to September, the percentage of variance of condition index explained by head length was 0.05% (r=0.023). Although these correlations between head length and condition index were statistically significant, this significance was probably due to the large sample size and unlikely to be biologically meaningful (Underhill 1999). The lack of any linear relationship between head length and the condition index confirms that Lubbe's (2008) approach is correct. This is also confirmed by Figure2 a,b.

Relationship between condition index and explanatory variables

Inter-annual and inter-island variability in condition

For the South African colonies overall, in comparison with the baseline level of the chick condition index at Robben Island in 2004, the condition index was poorer in 2008 by 0.179 ($t=-10.29$ $p<0.001$) and in 2009 by 0.2521 ($t=-15.13$; $p<0.001$) (Table 4). A separate comparison, setting 2008 as the reference level, showed that overall chick condition in 2009 was poorer than in 2008 ($t=-5.84$; $p<0.001$) for all South African colonies in this study.

The modelled chick condition index on Dassen (0.3558), Robben (0.3580), St Croix Island (0.3308) and Bird Islands (0.3746) in 2008 was poorer than the baseline level on Robben Island in 2004 (0.5367) (Table 5). The condition index at Dassen, Bird and St Croix Islands was not statistically different from that at Robben Island, the baseline colony (Table 4). Chick condition on Dyer Island was significantly poorer than that at the other colonies (Table 4). For example, the modelled condition index on Robben Island in 2008 was 0.3580, whereas on Dyer Island it was 0.2800 (Table 5).

The relationship between mass and total head length for chicks sampled throughout the study showed considerable variation (Figure 2a and b). Chick condition was generally lower at all islands during the course of the study than it was at Robben Island in 2004 (Figure 2a & b), with none of the colonies having a greater proportion of chick condition above 0.50 than that of Robben in 2004 (Table 6). For example, in 2004 on Robben Island, 52.5% of chicks had a body condition of 0.50 or more, which decreased to 27.56%

in 2008 and 32.57% in 2009. Only 25.36% of chicks on Dyer Island in 2008 had a body condition of over 0.50, decreasing to 17.44% in 2009 (Table 6).

Sample sizes from the Namibian colonies were too small to make statistical inferences. However, the range of observed condition indices was similar to that at South African colonies

Intra-annual variability in chick condition

Monthly patterns of variability for the condition index are shown as monthly means. To illustrate the extent of variability in chick condition during a year, the monthly pattern of the condition index is shown by half month and month for Robben Island 2009, the year and colony for which the largest sample size is available (Figure 3). Subsequent figures present data by month for every year/colony combination on single plots (Figure 4a and b).

Every colony in every year was characterized by large variation in mean chick condition between months and for corresponding months of successive years (Figures 3 and 4, Tables 2 and 3). On Robben Island in 2008, for example, mean chick condition varied from a mean minimum of –0.02 in April (n=103) to a mean maximum of 0.38 in both July (n=156) and August (n=79). However, in 2009, the following year, mean chick condition ranged from a mean minimum of –0.09 in November (n=21) to a mean maximum of 0.55 in September (n=159) (Tables 2 and 3). Each colony displayed a different seasonal pattern of mean monthly chick condition for both 2008 and 2009 (Figure 4).

On average, for the three breeding seasons 2004, 2008 and 2009 and for the South African colonies, chicks were in best condition in June (Table 7). Chick condition for all other months was significantly poorer than that in June, with condition in February ($p=0.002$), March ($p<0.001$), August ($p<0.001$), October ($p<0.001$) and November ($p<0.001$) being the months of overall poorest condition (Table 7). No data were available for December and January. There were insufficient data from Namibian colonies to make a similar comparison.

Hatching order

For the combined dataset of Dyer 2008, Dyer 2009 and Dassen 2009, once the effect of month and island had been removed, the condition index for A-chicks and singletons was not significantly different (t=–0.41, p=0.680). However, the condition of B-chicks was significantly depressed by 0.120 (t=–7.83, p<0.001) in relation to A-chicks (Figure 6, Table 8). There was no significant interaction between chick status and colony and year.

Relationship between mean condition index and its variability

The variability of mass of chicks at the five islands in 2008 and 2009, as related to total head length, is illustrated in Figure 2a and b. Also shown in Figures 2a and 2b are the 95% and 5% quantile regression lines computed by Lubbe (2008), from measurements made at Robben Island in 2004 by S. Bouwhuis (unpublished).

There were 236 sampling days with 10 or more observations during 2008 and 2009. The standard deviation of condition index was negatively correlated with the mean condition index for these 236 days (r=–0.192; p=0.003). This indicated that when the mean condition was good, the variability of the condition index was small, and when the mean condition was poor, the variability of the condition index was large.

Consequence of frequency of fieldwork

Tables 9 and 10 indicate the amount of variance explained by the model in relation to condition measured at different sampling intervals. Table 9 indicates that, for the combined dataset of Dassen Island 2009, Robben Island 2004, 2008, and 2009 and Dyer Island 2008 and 2009 over all months, daily intervals accounted for the greatest percentage of variance explained (26%).

The values of Akaike Information Criterian (AIC) increased from 38270 for daily sampling to 38509 for 30-day interval (ΔAIC=239). The difference in the AIC value from a daily sampling interval to a 15-day sampling interval (ΔAIC=82) was smaller than that from a daily (ΔAIC=239) or 15-day (ΔAIC=157) interval to that of a monthly interval (Table 9).

If the dataset is confined to the period April–September, the period of the year in which the largest number of chicks are present at most colonies in South Africa, the amount of variance explained decreases, as do the AIC values (Table 10). Again, the differences in

AIC values from daily sampling intervals to 15-day intervals were smaller than that from daily or 15-day to 30-day intervals. The variability in variance explained is less than that in the models in Table 9, with daily to 15-day intervals accounting for 23.4% to 18.4% of the variance explained for the winter sampling period (Table 10), compared to that of 25.6% to 19.4% for the entire period (Table 9).

Table 10 includes additional models run for all South African islands and years for which data were available from April to September. Colony alone only explained 4.3 % of the variance; between 2008 and 2009 chick condition accounted for 8.9 % of the variance in the model if the 2008 and 2009 year data for each colony was included. When 2008 and 2009 data for each colony was considered as a separate factor (Island), the model accounted for 9.6% of the variation in chick condition. The amount of variance explained by the model improved slightly when month factor was added to the model, and 10.8% of the variance was explained.

DISCUSSION

Body condition of adult penguins has been studied for a number of penguin species. Adult body condition at the start of incubation appears to be the most important factor in determining nest desertions in Magellanic penguins *S. magellanicus*, based on analyses of adult body mass (Yorio and Boersma 1994), while adult body condition in Galápagos penguins *S. mendiculus,* also evidenced by weight, is influenced by oceanic conditions, being enhanced during cold water conditions (Boersma 1998). Numata *et al.* (2000) found that foraging trip duration and risk of nest desertion of adult little penguins *Eudyptula minor* is significantly correlated with body condition. Clarke (2001) found that the foraging effort of Adélie penguins *Pygoscelis adeliae* is partitioned between the sexes and supported the hypothesis of Weimerskirch (2007) that body condition in long-lived seabirds plays a major role in determining allocation of resources between reproduction and survival.

These studies of adult penguins show that food availability for adult penguins prior to the onset of breeding is important in determining reproductive performance. In order to determine the quality of food resources during the breeding season, one can look at the season's overall breeding success, weigh the adults regularly throughout the season, or study the growth and condition of chicks, which provide an alternative index for the

local abundance of food around a colony and the parent's ability to utilise this food resource.

Studies of body condition in penguin chicks include that of Magellanic penguin chicks (Walker *et al.* 2005, Forero *et al.* 2002) and chinstrap *Pygoscelis antarctica* penguin chicks (Martin *et al.* 2006). These studies assessed body condition through standard morphometric measurements (Walker *et al.* 2005), as well as including sex as a factor since in both species there is sexual size dimorphism in body morphometrics. This study discussed findings which used condition index developed for African penguin chicks and applied it across spatial and temporal scales.

The choice of the year 2004 and Robben Island as the baseline for the condition index was based on data availability. In the context of the period 2001 to 2006, 2004 was an average breeding season on Robben Island (2004=64%, mean=66%, range=48–73%) in terms of fledging success (Barham *et al.* 2007, 2008a). This means that comparisons made in this study are not biased towards comparing to an above average breeding year, which would increase the likelihood of showing results that are poorer in comparison. An advantage of the 2004 data set was that it included only chicks that subsequently fledged successfully, and so represents the range of condition indices for fledged chicks. Condition index values lower than the minimum found in 2004 would thus indicate poor condition chicks that potentially would not fledge. No data were collected in December and January, which are months when few penguins breed in South Africa (Table 1).

An index derived from average growth rates is not considered an appropriate index to compare body condition across populations since average growth varies between regions and seasonally depending on food availability and environmental conditions (Jacob *et al.* 1996, Veen *et al.* 2004, Lubbe 2008). Studies of the condition of growing animals are difficult because of the variability in size from birth or hatching to independence (Lubbe 2008). The development of Veen's initial condition index by Lubbe (2008) is a promising technique to study the relative body condition of growing animals. The total head length was the measurement that best estimated body size for growing African penguin chicks since this structure was still growing when the penguins fledged unlike measurements such as flipper length which completed growth prior to fledging (Lubbe 2008). Total head length greater than 75mm was used as the best single measure of body size for African penguin chicks because (of all easily measured body structures) it

was closely linearly related to body mass until fledging (Lubbe 2008). This study applies Lubbe's index where the effect of size of the bird was shown to be removed, supported by a large dataset from multiple colonies.

In a study on African penguin chick growth rates, Sherley (2010) commented that additional investigation into the fit of growth curves for African penguins is warranted, with the possibility of using non-parametric approaches to analyse growth. The disadvantage of these approaches is that they require substantial data and measurements from hatching through to fledging (Sherley 2010) and multiple captures of individuals are required. In a rapidly declining, endangered species, disturbance to breeding birds and nests needs to be kept to a minimum and thus non-parametric approaches may not be ideal (Sherley 2010). Chick condition provides the opportunity to measure a random sample of chicks, less frequently than that needed for growth analyses and thus provides a promising avenue for assessing the quality of African penguin chicks, and providing information to food availability around breeding colonies.

Annual variability in chick condition

In a strongly seasonal environment with a short period in which food for breeding is abundant, we would anticipate that the body condition of chicks would be low at the beginning and the end of the season and peak in the middle for those parents which timed breeding perfectly to be raising chicks during peak food availability. However, the breeding season for African penguins is long, stretching over many months of the year.

The best explanation for a long breeding season is that there is no predictable time in the year at which it is best to breed. For African penguins, the time at which eggs are laid is two to three months prior to the peak energetic demands of chicks (Bouwhuis *et al.* 2007), and parents have to gamble on whether food will be readily available at the time when the demand for food will be at a maximum.

The Benguela Upwelling Ecosystem is one characterised by high variability (Crawford 1999, Field and Shillington 2004, van der Lingen *et al*. 2006, Hutchings *et al*. 2009). Large seasonal and inter-annual variability on pelagic fish biomass in the southern Benguela, especially since mid 1990s has been documented (van der lingen *et al*. 2006) and seabird parameters such as breeding success, chick growth and numbers breeding show high inter-annual variability in species using pelagic stocks (Adams *et al*. 1992,

Crawford *et al.* 1999, Mullers *et al.* 2009). One would thus expect African penguin chick condition to show temporal variability, which was the case in this study.

In this study, chick condition varied between years. Chick condition in 2008 and 2009 was poorer than that of 2004, with 2009 being poorest overall, especially within the Western Cape (Figure 4, Table 4). This suggests a reduction in the parent's ability to adequately provision for their chicks, through either a possible deterioration in overall feeding conditions in the Western Cape or a shift in fish availability for breeding penguins in the Western Cape since 2004.

In the first year of the fishing closure project (in 2008 when only Dassen Island was closed), chicks at the two west coast islands had similar average condition and Dyer Island on the south, the poorest condition. Chick condition in the Eastern Cape for that year was higher for the colonies in this study during 2008, and this was prior to closures effected in this area. In 2009, the situation varied with chicks at Dassen and Robben Islands having the better condition, those in the Eastern Cape intermediate condition and those at Dyer Island again the poorest condition.

Pichegru *et al.* (2010) analysed foraging data for 2008 and 2009 from Bird and St Croix Islands. They reported that penguins from St Croix (closed to small pelagic fishing in 2009) reduced their foraging effort by 25–30%, and that the core foraging area of these penguins shifted from 75% outside of the proposed closed area in 2008, when fishing was permitted, to >70% within the closed area in 2009 when fishing was prohibited there, suggesting a positive response to the fishing closure. The chick condition results however showed a decline in chick condition at the Eastern Cape colonies from 2008 to 2009, suggesting that although adults had probably reduced their foraging range, the quantity or quality of food available to them was inferior to that of 2008. For both St Croix (closed) and Bird Island (open), average adult body mass declined between 2008 and 2009, although this result was not significant (Pichegru *et al.* 2010).

Despite this variability, there does seem to be a trend toward declining chick condition similar to that observed in chick growth (Sherley 2010). Breeding success and nest survival decreased on Robben from 2008 to 2009 (Sherley 2010), and at all colonies, the numbers breeding were the lowest they had been on record in 2009 (Crawford *et al.*

2010). All these are factors are indicative of declining food availability of a decrease in optimal foraging conditions for African penguins.

Monthly variability in chick condition

This study applied Lubbe's index to a large dataset from multiple colonies. Results suggested that, overall, chick condition at South African African penguin colonies was best in June. Previous studies of African penguins in South Africa have shown peak breeding activity in winter (Crawford *et al*. 1999, Wolfaardt *et al*. 2008). Additionally, Sherley (2010) showed that overall chick growth rate was faster in June than during other months of the year.

There was however, substantial variability in individual years and at different colonies with peak condition for the breeding season at a specific colony occurring in different months. For example Dassen Island chick condition peaked in July in 2008 and in April in 2009. Robben Island chick condition showed a specific trend of peaking later in the year (Figure 5). Condition peaked in May and June during 2004, July and August during 2008 and September 2009. These findings are similar to that of the growth analysis of African penguins for the same period, where for the breeding seasons covered, there did not seem to be a period during the year that favoured chick rearing on the west coast (Sherley 2010). Dyer Island however was more consistent within the study period, with chick condition reaching a peak in June for both 2008 and 2009.

The variability of chick condition between months is likely to reflect a variable and unpredictable environment with variable feeding conditions throughout the year and indistinct seasons. Breeding is usually less synchronous in these environments, with an extended breeding season being observed in both Humboldt penguins (Paredes *et al*. 2002) and African penguins (Randall and Randall 1981, Wilson 1985, Kemper 2006) being observed. My results suggest that although it is preferable to raise chicks in winter, the breeding season can be flexible in response to changing food conditions.

African penguins are central place foragers, most penguins feed within 20km of their breeding colonies (Petersen *et al*. 2006, Ludynia 2007, Pichegru *et al*. 2010) and their foraging range is constrained by having to return to the nest to feed chicks. Chick condition is thus dependant on local prey availability, and given the variability in

abundance and distribution of pelagic fish stocks in space and time, chick condition will thus vary temporally (within and between years) and spatially.

Chick status

African penguin adults have asynchronous broods with a mean of 2.3 days elapsing between the first and second eggs hatching resulting in the second-hatched chick being, on average, 59% of the weight of the first-hatched chick (Williams and Cooper 1984, Seddon and van Heezik 1991, van Heezik and Seddon 1991). African penguin chicks are not siblicidal and although they compete for food resources, it is non- aggressive (van Heezik and Seddon 1996). The brood reduction hypothesis (Lack 1968) suggests that in an environment with unpredictable food resources, the inequalities among chicks as a result of asynchronous hatching may result in late-hatched chicks starving when food is scarce. Subsequently, growth and condition of second-hatched chicks is likely to be poorer than that of the first-hatched chick in periods of low food supply. This study showed a significant difference in condition between A and B chicks, and no significant relationship between A and single chicks, indicating that feeding conditions are poor when the B chick condition is poor. Similarly, that the condition of the single chick was similar to that of the A chick and not higher, indicates that feeding conditions may be poor.

Results of this study are similar to that reported in chick growth by Sherley (2010), Randall (1983) and Wolfaardt *et al*. (2008) where the B chicks tended to grow slower than that the A chick (as well as the singleton chick). Additionally, van Heezik and Davis (1990) found that growth of yellow-eyed penguin chicks was slower in two chick nests than that of single chick nests in a food poor year, but not in a year of good food availability. Similarly, Sherley (2010) found evidence to suggest that the ability of African penguins to rear two chicks decreased when food was less available on Robben Island from 2001-2009. These results suggest that the differential condition between A, B and singleton chicks may prove to be an additional useful indicator as to the status of local food availability around a breeding colony.

Sampling frequency for estimating chick condition

Because chick condition tends to fluctuate throughout the breeding season, measurements should be taken throughout the year rather than at one fixed date each year. Although my results show that a daily sampling protocol would yield the most

reliable chick condition data to allow an adequately analysis and interpretation of chick condition in relation to foraging conditions, such an intensive sampling schedule would cause excessive disturbance. Five day sampling intervals yield similarly reliable data and it is therefore recommended this interval may be used at African penguin colonies which are staffed by experienced personnel able to perform this task. For colonies which cannot be accessed or sampled as frequently, two-weekly sampling intervals provide sufficient information about chick condition throughout the year. The difference in variation explained from two-weekly intervals to monthly intervals from April to September is so low that monthly sampling during periods of bad weather, when colony access may be limited, is sufficient. To reduce possible effects of small sample sizes biasing results, a minimum of 50 chicks is recommended for each sampling date.

During the two years of chick condition monitoring, considerable variation in chick condition between years, seasons and months, as well as a lack of consistent trends in chick condition between colonies has been shown. It is difficult to interpret any direct effects of the fishing closures as a viable conservation measure for African penguins from these data alone, and it is essential that these results are analysed and interpreted in the light of results obtained for other parameters collected by the Island Closure Task Team, including population trends, foraging behaviour and ecology, diet, breeding success (including hatching and fledging success) and chick growth.

Concluding remarks and way forward

Chick condition varied over the course of the study, with 2009 being poorer overall than that of 2008 and both poorer than 2004. Whether this is indicative of a decreasing trend overtime should be monitored. The variability within colonies suggests that colonies do not respond uniformly with temporal differences in peak condition between Dassen and Robben Islands, only 50km apart for example, being observed.

The condition index developed by Lubbe (2008) provides a tool to assess chick condition for samples of chicks of unknown ages, of different sizes, and allows for spatial and temporal comparisons to be made. There was significant spatial and temporal variability in chick condition, between years, across months and between successive sampling dates. This suggests that this index could be a useful indicator of feeding conditions over periods of about two weeks. Furthermore, relating chick condition to the foraging behaviour of breeding adults would give additional insight into the local

availability of food, the cost to the breeding adult, which is ultimately reflected by chick condition, growth and number of chicks fledged. Boersma *et al*. (2009) found that more chicks were reared in colonies where the penguins could feed close to the colony compared to those penguins that had to feed further from the colony.

Fish catch can be considered an index as to the local availability of food around a breeding colony. Future directions of this work include relating chick condition to catch around the colony throughout a breeding season. I recommend the institution of small scale fish surveys in the vicinity around breeding colonies utilised by foraging breeding African penguins. Continued chick condition studies around these colonies will be a useful dataset with which to relate these small scale surveys.

It is questionable whether chicks below the 5% quantile line, i.e. with a condition index below 0 are able to recover and fledge successfully (Lubbe 2008). The next phase in this study will be to monitor the condition of 'known' chicks in attempt to estimate a 'starvation line' (Lubbe 2008). An established conservation intervention for African penguins is the removal of abandoned, end of season chicks to be hand-reared and released (Parsons and Underhill 2005, Parsons *et al*. 2007, Barham *et al*. 2008b). I recommend that the decision to intervene needs to be based on criteria that make use of the condition index. We should determine the lowest level which chick condition can reach below which a chick cannot be hand reared to fledging and survive to breed successfully. The 'condition graphs' (Figure 2a and b) enable field observers to plot the relevant morphological measurements of individual chicks immediately. This provides an indication of chick condition as measured by Lubbe's (2008) condition index.

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Table 1: Summary of African penguin chick condition measurements for Namibian (Halifax and Mercury) and South Africa (Dassen, Robben, Dyer, St Croix and Bird) African penguin breeding colonies mentioned in the text, for the 2008 and 2009 breeding seasons, including data from Robben Island in 2004. (Measurements with Head Length < 75mm were removed from analysis and are not included in this table).

Colony and year	Total sample size	Earliest sampling date	Last sampling date	Number of sampling dates	Min sample size per sampling date	Max sample size per sampling date	Mean sample size per sampling date	Mode sample size per sampling date	Largest gap between sampling dates (day)
Halifax Island 2008	10	26/03/2008	26/03/08	1	10	10	10	N/A	N/A
Halifax Island 2009	34	12/02/2009	1/09/2009	6	2	8	6	6	170
Mercury Island 2008	20	3/03/2008	7/03/2008	2	8	12	10	N/A	4
Mercury Island 2009	28	2/04/2009	21/09/2009	4	1	15	7	N/A	167
Dassen Island 2008	393	30/04/2008	21/10/2008	20	2	87	20	2	26
Dassen Island 2009	947	16/02/2009	15/10/2009	43	1	64	22	24	27
Robben Island 2004	1168	22/04/2004	20/10/2004	92	1	39	13	4	14
Robben Island 2008	762	2/04/2008	19/11/2008	35	1	52	22	30	21
Robben Island 2009	1176	5/03/2009	19/11/2009	64	1	67	18	11	14
Dyer Island 2008	978	28/03/2008	26/10/2008	32	3	60	31	11	11
Dyer Island 2009	883	28/03/2009	20/11/2009	33	2	101	27	6	14
St Croix 2008	179	28/05/2008	23/11/2008	5	27	45	36	27	104
St Croix 2009	245	28/03/2009	15/10/2009	6	17	79	41	N/A	68
Bird Island 2008	192	15/05/2008	17/11/2008	5	31	48	38	31	92
Bird Island 2009	272	22/03/2009	13/10/2009	8	14	61	34	N/A	56

Table 2: Summary statistics of chick condition of African penguins in 2004 at Robben Island and in 2008 at Dassen, Robben, Dyer, St Croix and Bird Islands, South Africa, and at Mercury and Halifax Islands, Namibia.

Colony	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Annual
Dassen 08											
Min			-0.21	-0.46	-1.14	-1.04	-0.72	-0.72	-0.63		-1.14
Lower quantile			0.18	0.23	-0.14	0.32	0.02	-0.08	-0.09		0.02
Median			0.30	0.41	0.10	0.55	0.32	0.20	0.12		0.34
Upper quantile			0.41	0.63	0.42	0.80	0.64	0.59	0.30		0.60
Max			0.76	1.42	1.04	1.66	1.65	1.66	0.92		1.66
Mean			0.28	0.45	0.11	0.53	0.36	0.24	0.13		0.32
SD			0.25	0.39	0.44	0.43	0.51	0.47	0.37		0.46
n			21	59	87	92	62	45	25		393
Robben 04											
Min			-0.35	-0.07	-0.54	-0.85	-0.19	-0.21	-0.37		-0.85
Lower quantile			-0.01	0.39	0.41	0.24	0.31	0.18	-0.05		0.33
Median			0.08	0.57	0.58	0.44	0.48	0.34	0.09		0.52
Upper quantile			0.14	0.73	0.76	0.63	0.67	0.47	0.40		0.70
Max			0.36	1.55	1.39	1.27	1.10	0.99	1.65		1.65
Mean			0.05	0.58	0.58	0.42	0.48	0.33	0.21		0.51
SD			0.24	0.27	0.28	0.33	0.27	0.22	0.43		0.31
n			6	281	459	226	99	62	35		1168
Robben 08											
Min			-1.10	-0.90	-0.39	-1.10	-1.20	-1.07	-0.47		-1.20
Lower quantile			-0.24	0.00	0.04	0.14	0.17	0.10	-0.01		0.05
Median			0.01	0.17	0.28	0.38	0.38	0.32	0.14		0.27
Upper quantile			0.20	0.45	0.46	0.62	0.63	0.51	0.34		0.52
Max			0.88	0.98	1.17	1.98	1.18	1.07	0.87		1.98
Mean			-0.02	0.19	0.25	0.38	0.38	0.29	0.16		0.27
SD			0.38	0.32	0.29	0.42	0.38	0.35	0.30		0.38
n			103	90	114	156	79	89	44		762
Dyer 08											
Min		-1.48	-1.58	-0.45	-0.82	-0.50	-1.37	-0.74	-2.33		-2.33
Lower quantile		-1.38	0.28	0.19	0.27	0.14	-0.16	-0.17	-0.12		0.05
Median		0.19	0.46	0.41	0.46	0.35	0.08	0.04	0.10		0.28
Upper quantile		0.39	0.66	0.59	0.71	0.51	0.25	0.21	0.28		0.50
Max		0.79	2.07	0.98	1.75	1.35	0.85	0.80	0.87		2.07
Mean		-0.26	0.41	0.40	0.46	0.32	0.04	0.04	0.04		0.25
SD		0.94	0.47	0.29	0.34	0.30	0.33	0.31	0.42		0.40
n		11	114	114	157	211	177	113	81		978
St Croix 08											
Min				-1.30	-0.15			0.07	-0.77	-0.34	-1.30
Lower quantile				0.06	0.46			0.43	0.34	0.14	0.27
Median				0.31	0.69			0.73	0.67	0.42	0.52
Upper quantile				0.57	0.82			0.88	0.83	0.61	0.78
Max				1.06	1.36			1.44	1.69	0.92	1.69
Mean				0.30	0.64			0.71	0.61	0.37	0.51
SD				0.45	0.33			0.33	0.43	0.33	0.41
n				38	27			27	45	42	179
Bird 08											
Min				-0.51	-0.15			-0.48	-0.38	-0.48	-0.51
Lower quantile				0.15	0.16			0.27	0.24	0.00	0.18
Median				0.46	0.38			0.48	0.43	0.22	0.41
Upper quantile				0.69	0.60			0.69	0.62	0.41	0.62
Max				0.97	1.19			1.20	1.18	0.75	1.20
Mean				0.41	0.42			0.46	0.44	0.21	0.40
SD				0.38	0.32			0.34	0.31	0.30	0.33
n				31	43			39	48	31	192

Colony	Feb	March	Apr	May	June	Jul	Aug	Sept	Oct	Nov	Annual
Mercury 08											
Min		-0.16									-0.16
Lower quantile		0.04									0.04
Median		0.24									0.24
Upper quantile		0.49									0.49
Max		1.06									1.06
Mean		0.28									0.28
SD		0.33									0.33
n		20									20
Halifax 08											
Min		0.45									0.45
Lower quantile		0.58									0.58
Median		0.57									0.57
Upper quantile		0.59									0.59
Max		1.10									1.10
Mean		0.74									0.74
SD		0.22									0.22
n		10									10

Table 3: Mean chick condition of African Penguin in 2009 at Dassen, Robben, Dyer, St Croix and Bird Islands and in 2004 at Robben Island, South Africa, and at Mercury and Halifax Islands, Namibia.

Colony	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Annual
Dassen 09											
min	-0.13	-1.02	-0.79	-0.37	-0.91	-0.58	-1.02	-0.97	-0.91		-1.02
lower quartile	0.00	-0.02	0.23	0.19	0.23	-0.09	-0.15	0.08	0.05		0.05
median	0.06	0.20	0.52	0.40	0.44	0.14	0.25	0.29	0.28		0.31
upper quartile	0.15	0.46	0.70	0.57	0.68	0.41	0.46	0.54	0.38		0.55
max	0.41	1.24	1.38	0.99	2.06	1.06	1.15	1.32	0.84		2.06
mean	0.09	0.20	0.47	0.37	0.44	0.18	0.17	0.30	0.12		0.28
SD	0.16	0.43	0.36	0.30	0.43	0.35	0.43	0.44	0.42		0.42
n	14	225	139	74	147	120	115	71	42		947
Robben 04											
min			-0.35	-0.07	-0.54	-0.85	-0.19	-0.21	-0.37		-0.85
lower quartile			-0.01	0.39	0.41	0.24	0.31	0.18	-0.05		0.33
median			0.08	0.57	0.58	0.44	0.48	0.34	0.09		0.52
upper quartile			0.14	0.73	0.76	0.63	0.67	0.47	0.40		0.70
max			0.36	1.55	1.39	1.27	1.10	0.99	1.65		1.65
mean			0.05	0.58	0.58	0.42	0.48	0.33	0.21		0.51
SD			0.24	0.27	0.28	0.33	0.27	0.22	0.43		0.31
n			6	281	459	226	99	62	35		1168
Robben 09											
min		-0.63	-1.16	-0.52	-0.47	-0.83	-1.42	-0.81	-0.38	-1.13	-1.42
lower quartile		-0.16	-0.03	0.27	0.14	-0.11	0.12	0.34	0.11	-0.29	0.05
median		0.06	0.28	0.47	0.34	0.23	0.40	0.60	0.35	0.07	0.32
upper quartile		0.24	0.47	0.66	0.61	0.51	0.60	0.78	0.53	0.25	0.58
max		0.67	1.50	1.34	1.30	1.12	1.43	1.34	1.22	0.42	1.50
mean		0.03	0.21	0.45	0.35	0.21	0.34	0.55	0.32	-0.09	0.30
SD		0.28	0.40	0.34	0.36	0.40	0.41	0.34	0.34	0.45	0.40
n		123	203	98	138	180	181	159	73	21	1176
Dyer 09											
min		-0.05	-0.75	-0.99	-1.19	-1.18	-0.57	-0.47	-0.84	-0.79	-1.19
lower quartile		0.12	-0.10	-0.04	0.13	-0.04	-0.16	-0.08	-0.20	0.10	-0.05
median		0.24	0.18	0.17	0.32	0.19	0.07	0.15	0.04	0.23	0.20
upper quartile		0.36	0.55	0.37	0.53	0.40	0.27	0.35	0.21	0.50	0.40
max		0.52	0.92	0.79	1.32	1.48	0.92	0.98	0.77	1.15	1.48
mean		0.24	0.18	0.17	0.30	0.19	0.07	0.14	0.00	0.25	0.18
SD		0.18	0.43	0.33	0.33	0.35	0.30	0.31	0.34	0.36	0.34
n		8	34	118	178	122	154	103	57	109	883
St Croix 09											
min		-0.60	-0.61	-0.51	0.08		-0.86		-0.52		-0.86
lower quartile		0.05	0.03	-0.17	0.26		-0.04		0.03		-0.01
median		0.27	0.33	0.05	0.40		0.12		0.22		0.23
upper quartile		0.48	0.56	0.28	0.56		0.30		0.40		0.48
max		0.68	1.16	0.80	1.04		0.78		0.99		1.16
mean		0.24	0.30	0.09	0.44		0.14		0.22		0.23
SD		0.30	0.40	0.33	0.23		0.32		0.33		0.35
n		32	79	40	17		43		34		245
Bird 09											
min											
lower quartile											
median											
upper quartile											
max											
mean											
SD											
n											

Colony	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Mercury 09										
min			-0.34					-0.89	-0.34	
lower quartile			-0.17					0.41	-0.17	
median			0.07					0.55	0.07	
upper quartile			0.27					0.86	0.27	
max			0.33					1.20	0.33	
mean			0.03					0.53	0.03	
SD			0.31					0.44	0.31	
n			4					24	4	
Halifax 09										
min	-0.73	-0.71					-0.08	-0.73	-0.71	
lower quartile	-0.06	0.08					0.19	-0.06	0.08	
median	0.25	0.14					0.61	0.25	0.14	
upper quartile	0.47	0.51					0.95	0.47	0.51	
max	0.68	0.89					1.05	0.68	0.89	
Mean	0.16	0.19					0.54	0.16	0.19	
SD	0.42	0.55					0.42	0.42	0.55	
N	14	6					14	14	6	

Table 4: Results of the regression analysis that compares African penguin chick condition at South African colonies for 2008 and 2009 to the reference level of Robben Island (reference colony) in 2004 (reference year).

Parameter	estimate	s.e.	t(4456)	t pr.
Constant	0.5367	0.0111	48.44	<.001
Year 2008	–0.1787	0.0174	–10.29	<.001
Year 2009	–0.2521	0.0167	–15.13	<.001
Colony Dassen	–0.0022	0.0173	–0.13	0.897
Colony Dyer	–0.0780	0.0153	–5.09	<.001
Colony Bird	0.0166	0.0272	0.61	0.542
Colony StCroix	–0.0272	0.0304	–0.89	0.371

Table 5: Modelled African penguin chick condition indices based on the results in Table 4.

Parameter	2004	2008	2009
Dassen		0.3558	0.2824
Robben	0.5367	0.3580	0.2846
Dyer		0.2800	0.2066
Bird		0.3746	0.3012
St Croix		0.3308	0.2574

Table 6: Proportion of African penguin chicks with body condition index larger than 0.5 at selected South African breeding colonies.

Colony	n	n (≥50%)	%(≥50%)
Robben 2004	1168	613	52.48
Robben 2008	762	210	27.56
Robben 2009	1176	383	32.57
Dyer 2008	978	248	25.36
Dyer 2009	883	154	17.44
Dassen 2008	393	136	34.61
Dassen 2009	947	276	29.14
Bird 2008	192	74	38.54
Bird 2009	272	64	23.53
St Croix 2008	245	54	22.04
St Croix 2009	179	92	51.4

Table 7: The overall monthly pattern of African penguin chick condition at South African penguin breeding colonies mentioned in the text and for all years (2004, 2008 and 2009), relative to June as baseline month. df=7195.

Month	Condition Index	SE	T	p-value
February	–0.3123	0.0996	–3.14	0.002
March	–0.2314	0.0222	–10.45	<.001
April	–0.1089	0.0173	–6.29	<.001
May	–0.0403	0.0154	–2.61	0.009
June	0			
July	–0.0816	0.0148	–5.52	<.001
August	–0.1505	0.0159	–9.48	<.001
September	–0.0775	0.0173	–4.48	<.001
October	–0.1339	0.0190	–7.03	<.001
November	–0.1197	0.0279	–4.30	<.001

Table 8: Variability of African penguin chick condition in A, B and Singleton chicks for Dassen Island in 2009, Robben Island in 2009 and Dyer Island in 2008 and 2009.

Parameter	estimate	s.e.	t(1796)	t pr.
Constant	0.3135	0.0107	29.24	<.001
ABS B	–0.1196	0.0153	–7.83	<.001
ABS S	–0.0076	0.0185	–0.41	0.680

Table 9: Amount of variation of condition index explained for Dassen 2009, Robben 2004, 2008, 2009, Dyer 2008, 2009 over all months, grouping the data for in various sampling frequencies.

Sampling Frequency	Sample	Akaike	Variance Explained (%)
1 day interval	296	38270	25.6
5 day interval	192	38307	23.9
10 day interval	127	38326	22.8
15 day interval	91	38352	22.0
20 day interval	70	38347	21.8
30 day interval	49	38509	19.4

Table 10: Percentage variance explained in African penguin chick condition variability for different models for Dassen, Robben, Dyer, St Croix and Bird Islands, South Africa from April–September (2008, 2009 and Robben 2004).

Model	Terms	AIC	%Variance Explained
Colony*Year*1day	270	39147	23.4
Colony*Year*5day	173	39161	22.0
Colony*Year*10day	123	39173	21.2
Colony*Year*15day	95	39202	20.4
Colony*Year*20day	80	39193	20.4
Colony*Year*Month	57	39315	18.4
Colony*year and month (April – September)	13	28286	11.5
Colony*Year*Month	9	28313	10.8
Year*Month	5	28339	10.2
Island Effect*Year Effect (each island in each year considered separately)	10	28376	9.6
Colony Effect and Year Effect	6	28404	8.9
Year	2	28433	8.3
Colony	4	28622	4.3

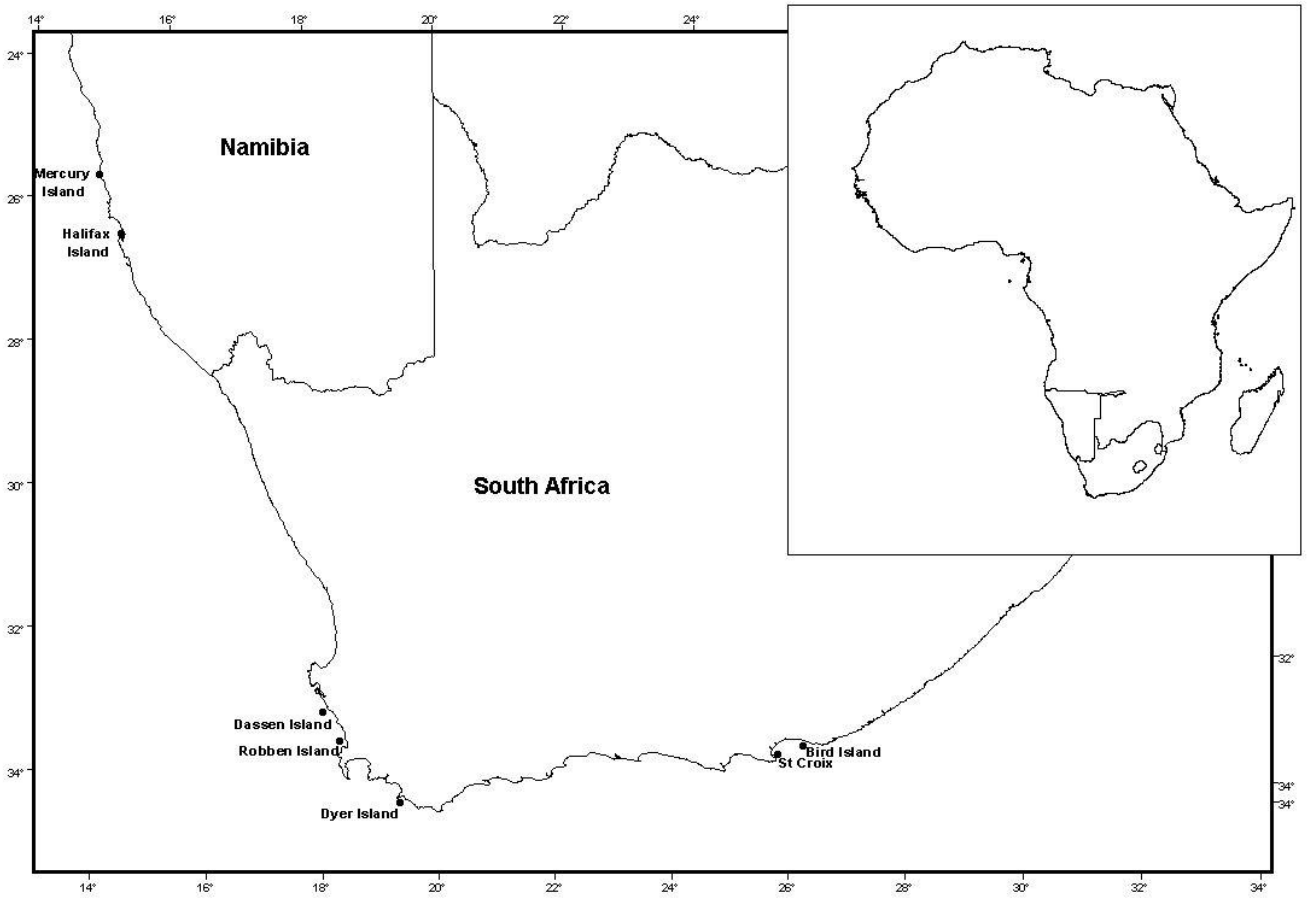


Figure 1: The south-west coast of Africa, indicating the location of African penguin breeding localities in Namibia and South Africa referred to in the text.

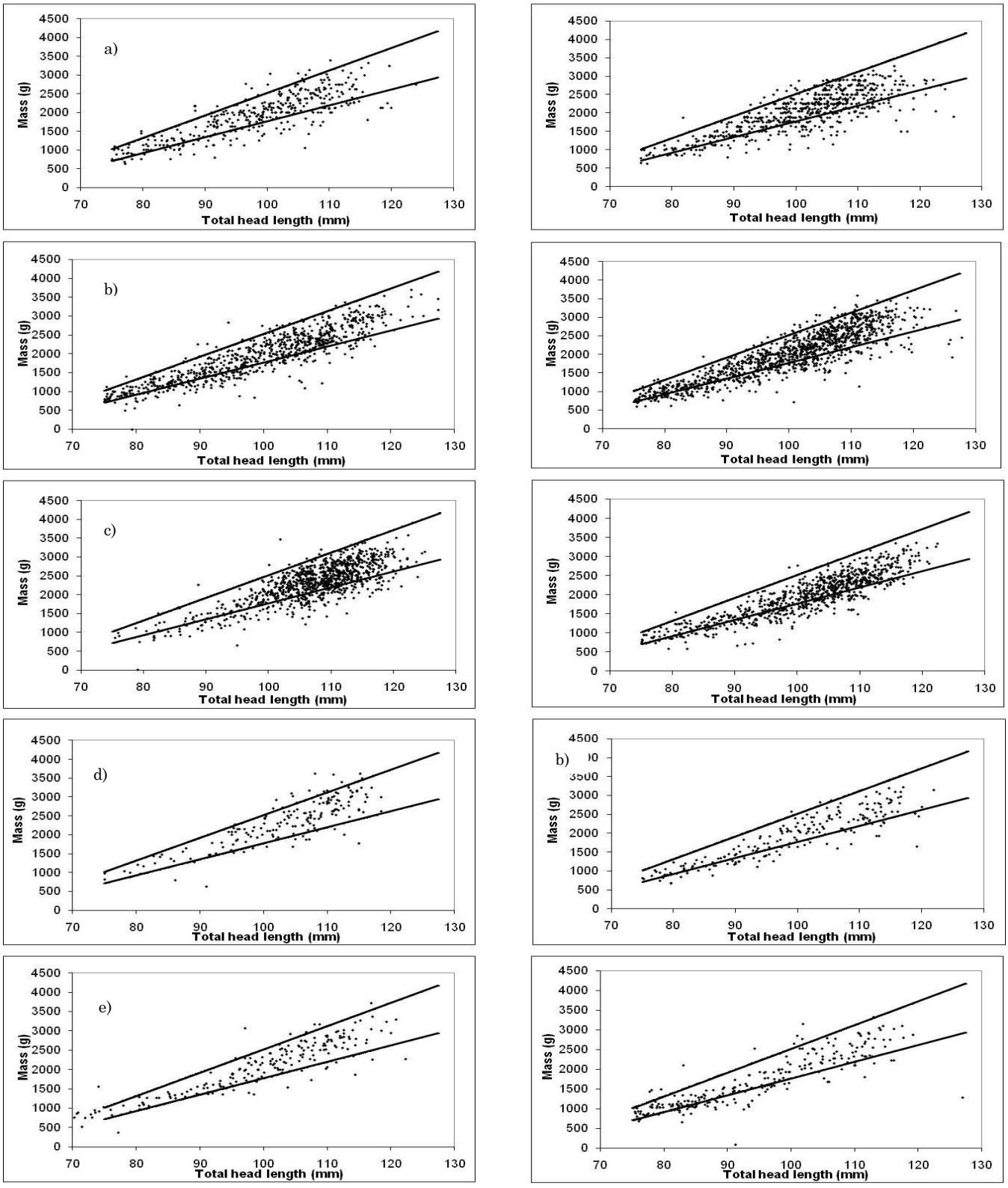


Figure 2a: The variability of mass of African penguin chicks as related to head length in 2008 (left), 2009 (right) for a) Dassen b) Robben c) Dyer d) St Croix and e) Bird Islands in South Africa. The 95% (top line) and 5% (lower line) quantile values obtained by S. Bouwhuis (unpublished) at Robben Island in 2004 are shown on each plot for comparison.

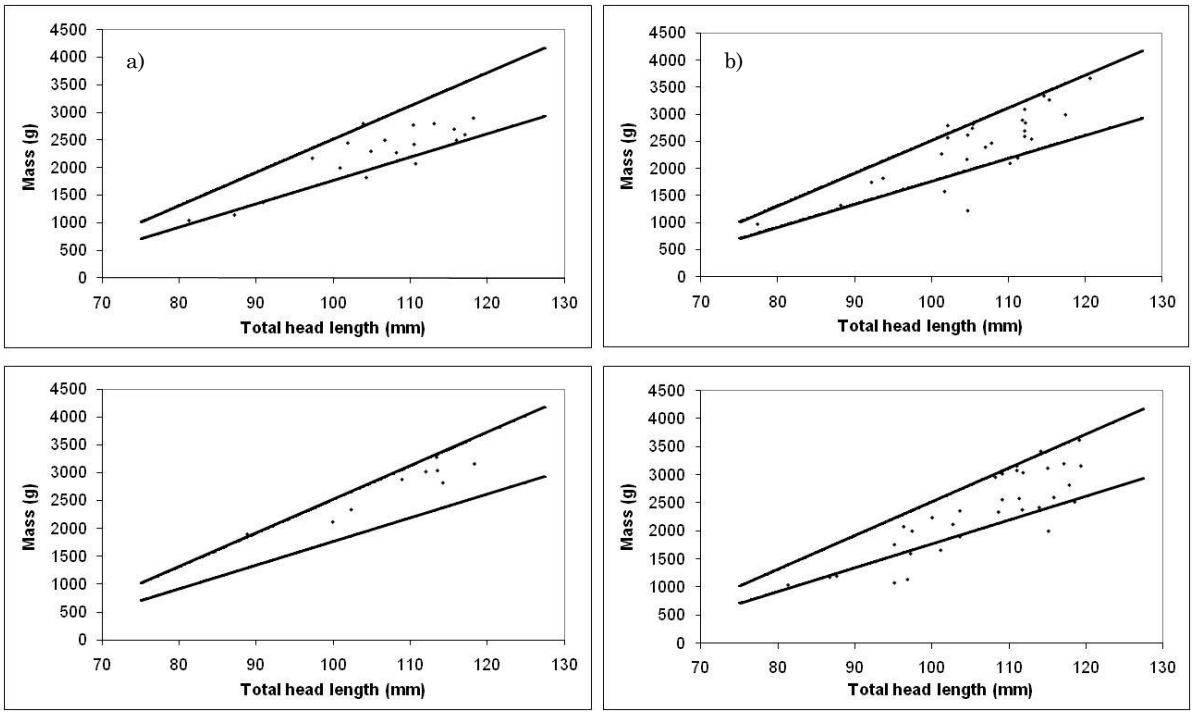


Figure 2b: The variability of mass of African penguin chicks as related to head length in 2008 (left) and 2009 (right) for a) Mercury and b) Halifax Islands in Namibia. The 95% (top line) and 5% (lower line) quantile values obtained by S. Bouwhuis (unpublished) at Robben Island in 2004 are shown on each plot for comparison.

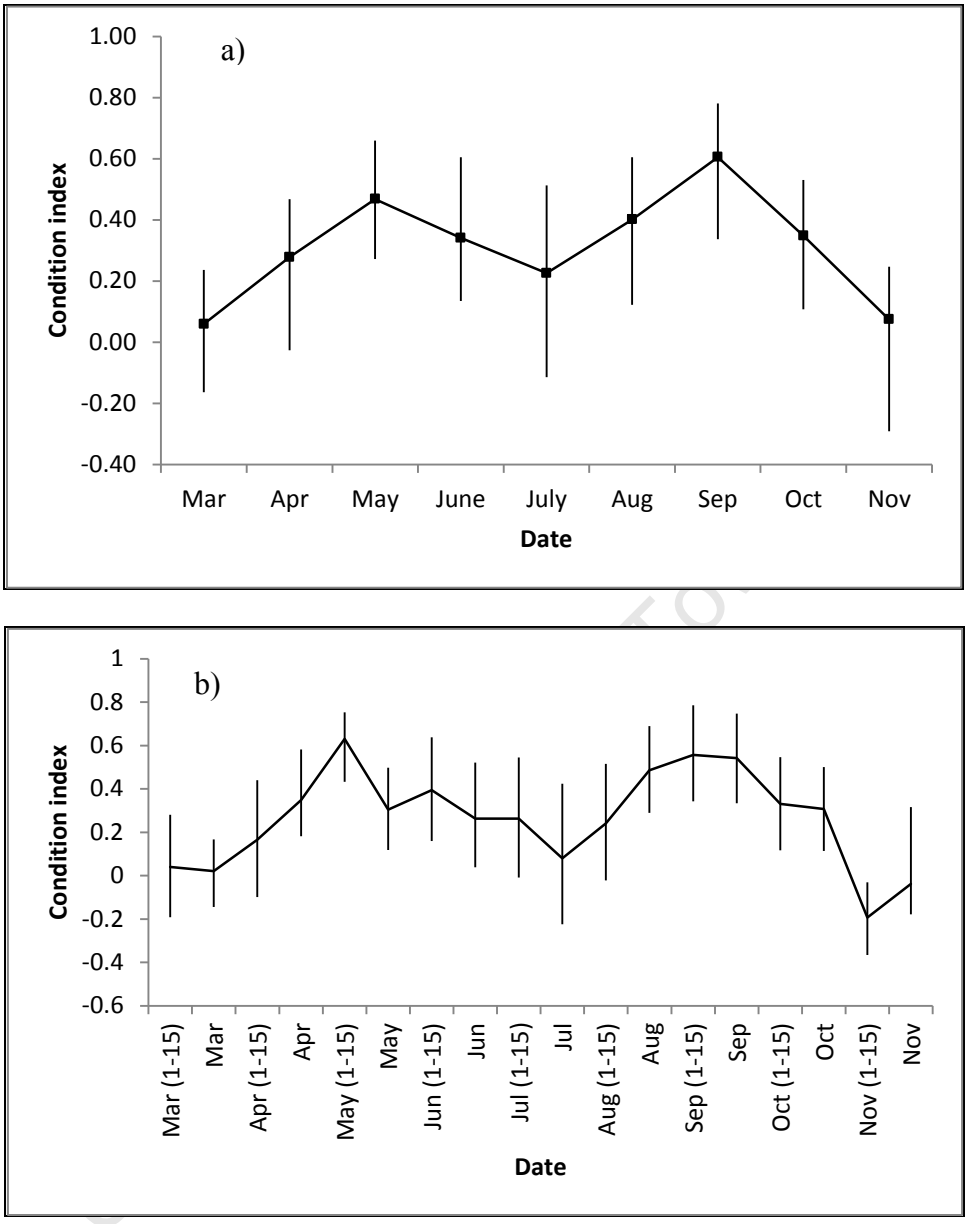


Figure 3: Mean monthly (a) and bi-monthly (b) African penguin chick condition indices for Robben Island in 2009 (vertical bars denote upper and lower quartile values).

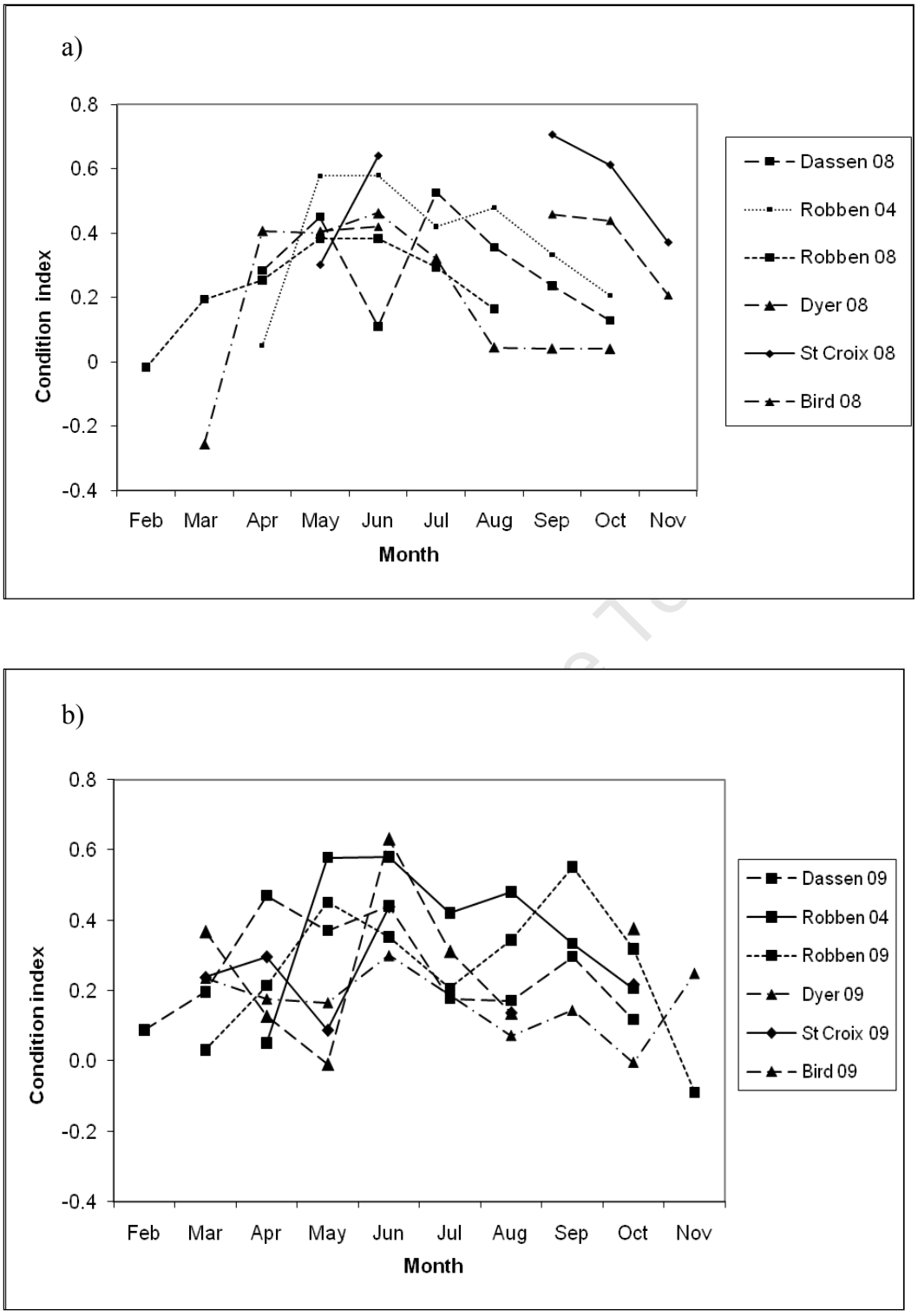


Figure 4: Mean chick condition for African penguins for a) 2008 and b) 2009 at Dassen Island, Robben Island, Dyer Island, St Croix Island and Bird Island. Robben Island 2004 chick condition is included in both graphs as a reference year.

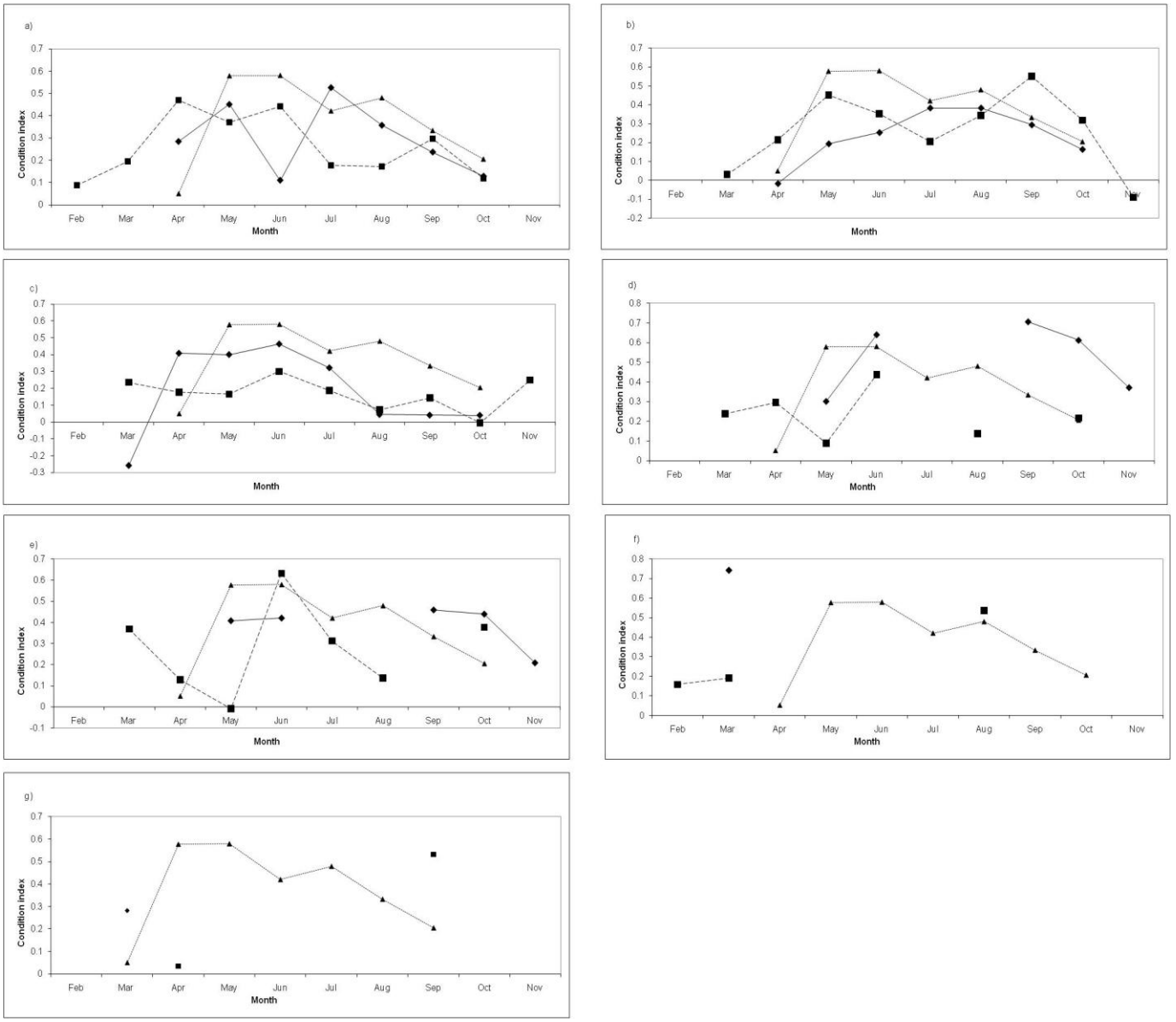
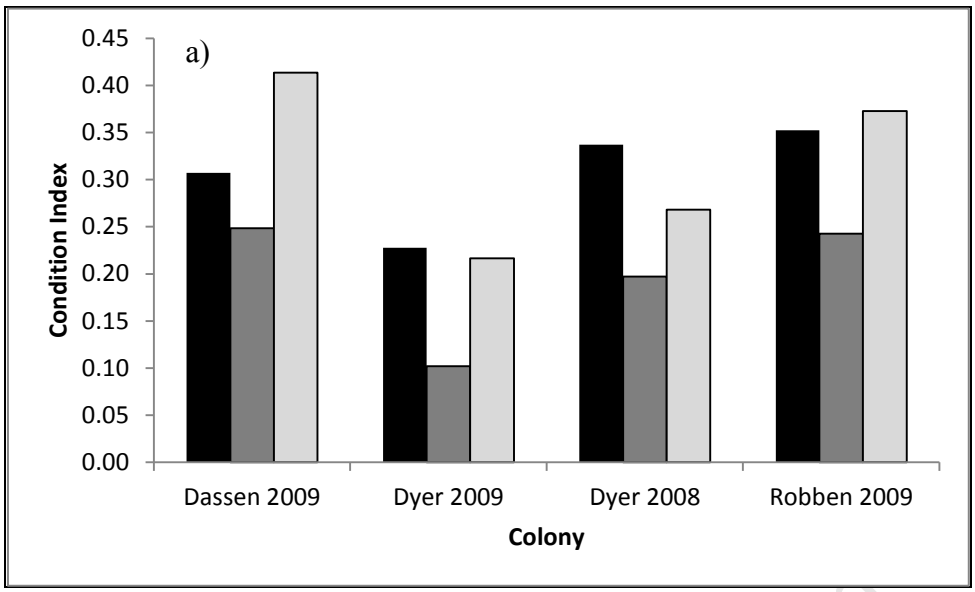


Figure 5: Comparison of African penguin chick condition for 2008 (diamonds) and 2009 (squares) for a) Dassen b) Robben c) Dyer d) St Croix e) Bird f) Halifax and g) Mercury Islands. Robben Island 2004 (triangles) is included as a reference year.



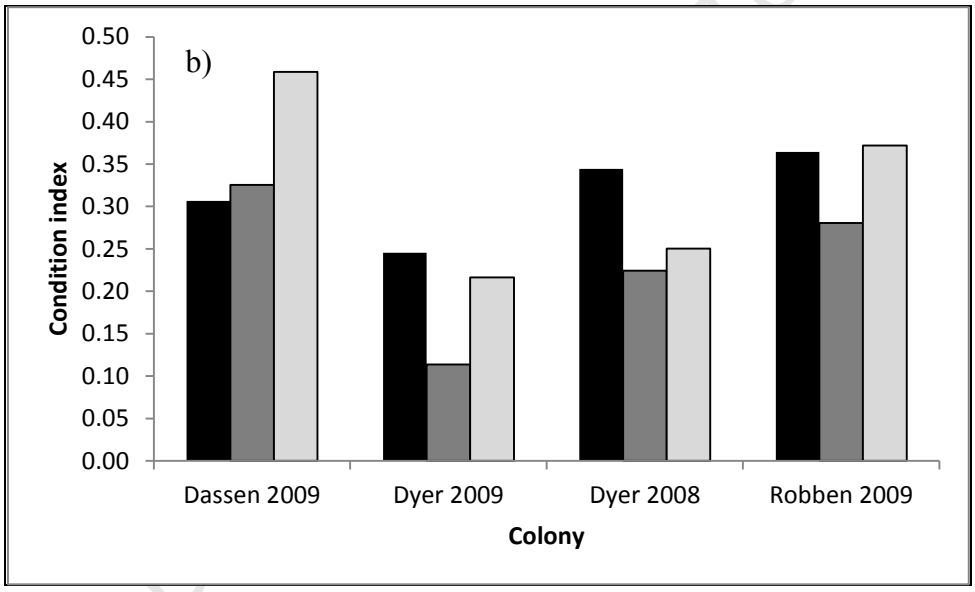


Figure 6: Mean (a) and median (b) African penguin chick condition for A-chick (black), B-chick (dark grey) and Singleton (light grey) for Dassen Island in 2009, Dyer Island in 2008 and 2009 and Robben island in 2009.

CHAPTER 5

FORAGING AREA AND DIVING BEHAVIOUR OF BREEDING AFRICAN PENGUINS ON DYER ISLAND

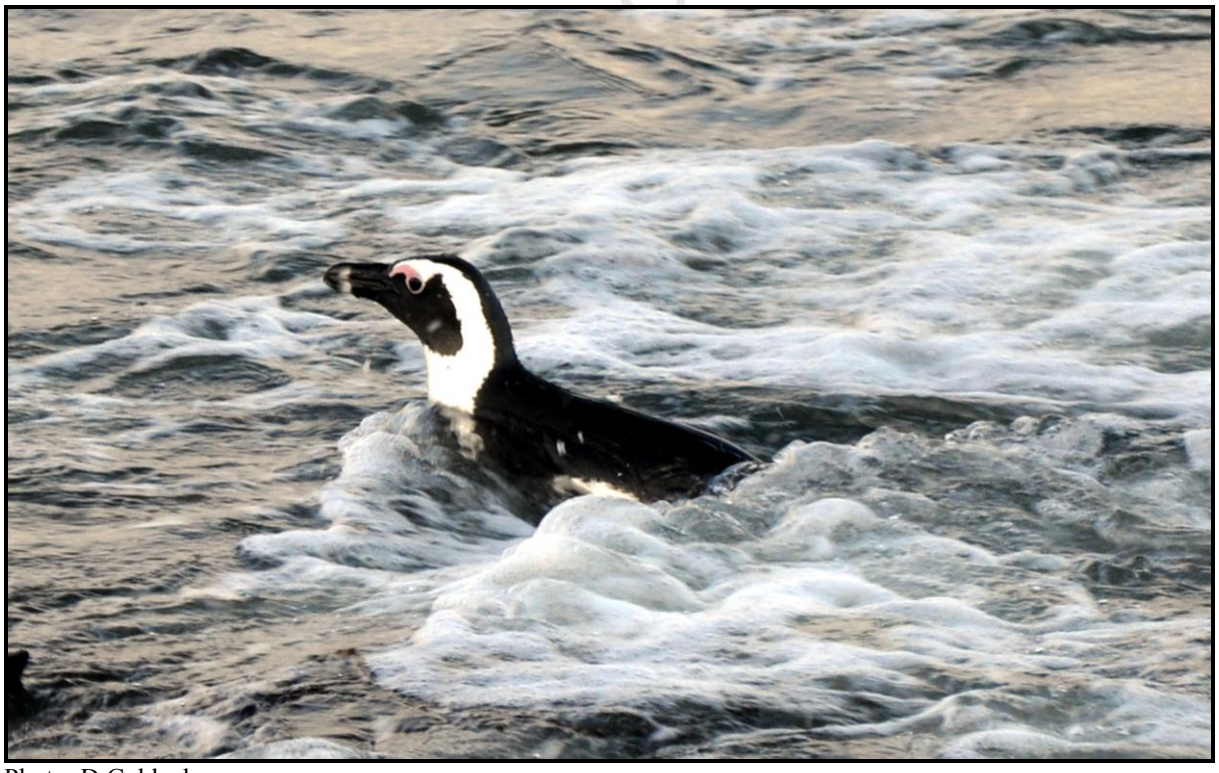


Photo: D Geldenhuys

FORAGING AREA AND DIVING BEHAVIOUR OF BREEDING AFRICAN PENGUINS ON DYER ISLAND

ABSTRACT

The foraging area and diving behaviour of breeding African penguins *Spheniscus demersus* on Dyer Island was studied in 2008, 2009 and 2010. There was no difference in foraging range, distance travelled or trip duration between years, suggesting that feeding conditions had been similar throughout the study period. Mean depth, mean foraging bottom time, mean foraging duration and foraging efficiency differed between years. In comparison with other foraging studies of African penguins, Dyer Island penguins had greater foraging range, longer trip duration and travelled further. Furthermore, Dyer Island penguins had more overnight trips than studies conducted at other colonies. That chick condition at Dyer Island is shown to be consistently poor compared to that of other colonies, may suggest that food is a limiting factor at Dyer Island.

KEY WORDS

African penguin, diving behaviour, Dyer Island, foraging area, trip duration

INTRODUCTION

The African penguin *Spheniscus demersus* was classified as "Endangered" in 2010 as a result of a rapid population decline since 2004 (BirdLife International 2010, Crawford *et al*. in press). The species declined by at least 90% during 20th century (Crawford *et al*. 2001). Despite a promising increase in the population from 1987 to 2004, especially at the larger breeding colonies of Dassen Island and Robben Island (Underhill *et al*. 2006), the decline from 2004 resulted in the species being at its lowest level ever recorded in 2010 (Crawford *et al.* in press).

The trend in the African penguin population has generally been similar at the breeding colonies in South Africa, with regionally coherent population trends related to long-term changes in the abundance and distribution of its main prey, Cape anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* fish stocks (Crawford 1998, Crawford *et al.* 2001, Underhill *et al.* 2006, Crawford *et al.* 2008a,b). These regional trends however,

did not hold true for Dyer Island. The collapse in the Dyer Island population took place in the late 1970s (Shelton *et al.* 1984); this was linked to the declining numbers of anchovy off the south coast (Crawford 1998). At the same time however, two coastal mainland breeding sites were formed (Boulders and Stony Point) and Robben Island on the west coast was re-colonised (Crawford *et al.* 1995, 1999). These three sites are only 60 km (Stony Point), 100 km (Boulders) and 160 km (Robben Island) from Dyer Island (Figure 1).

The recent decline of the African penguin is primarily thought attributable to the decline in local food sources, through a combination of an eastward displacement of pelagic fish stocks (Fairweather *et al*. 2006, van der Lingen *et al*. 2006), and competition with commercial fisheries (Crawford *et al*. in press). So, while the west coast colonies of Dassen Island and Robben Island decreased, seemingly as a result of this eastward shift and reduced local abundance of pelagic fish, an increase in the Dyer Island African penguin population could have been expected. This however has not been observed, and the question remains why.

The distribution of African penguins is consistent with the distribution of pelagic shoaling fish which are found within the 200 m contour (Crawford 1981). An adequate food supply is essential to maintain a stable population; however studies of pelagic fish stocks are difficult to conduct, due to the nature of the species in question and the high cost of the surveys. Studies of the foraging behaviours of seabirds can be used to provide insight into the local availability of fish (Wilson 1985a, Cherel and Weimerskirch 1995, Petersen *et al.* 2006, 2010, Ludynia 2007), and provide an indication of the colony health status for breeding seabirds (Mullers and Navarro 2010). The foraging behaviour of breeding African penguins is influenced by increasing food demands of chicks as they get older, as well as variation in prey abundance and distribution (Heath and Randall 1989, Petersen *et al.* 2006). African penguins are central place foragers (Davis and Renner 2003) and so are restricted in the area they can cover within a single foraging trip, and are thus reliant on a predictable food source in close proximity to their colony (Wilson 1985a, Tremblay and Cherel 2003).

African penguin foraging behaviour is impacted by its flightlessness, being unable to cover as large an area as an aerial seabird in the search for its pelagic food (Wilson 1985a) and is also impacted by their limited knowledge of the spatial distribution of

their prey (Navarro 2010). Hunt and Schneider (1987) stated that predictability of food resources is time-scale dependant; it is predictable at mesoscales (there are fish available annually in the Benguela Upwelling Ecosytem) but becomes increasingly less predictable on decreasing spatial and temporal scales (fish availability on a weekly scale in the 20-km feeding area around a breeding colony). In addition, fine-scale patches of food resources are nested within patches at broader scales (Fauchald 1999), which has an impact on the search strategy of foraging predators (Grünbaum 1998). The manner in which animals adjust their movement patterns in relation to their environment is important in understanding aspects of their ecology, and in this case, their foraging ecology (Navarro 2010). One approach in analysing animal movements is that of looking for patterns that emerge from the data (the other involves fitting a theoretical model that is hoped to provide a realistic account of the animal's movement) (Navarro 2010). The methods developed to analyse the movement patterns are based on measuring tortuosity or sinuosity of the movement path (Navarro 2010). Seabirds can be expected to travel a long distance, with a low turning path before a prey patch is encountered. Once the patch is found, a smaller scale search pattern with a path of higher turning rates, covering smaller distances at a reduced speed to maximise prey encounter rate can be expected (Fauchald 2009). This is known as area restricted search (ARS) which corresponds to a biased random walk (Grünbaum 1998). Haury *et al*. (1978) devised a hierarchical method of analysing movement at different scales where fine-scale movement includes that which occurs at 1–1000 m; course scale at 1–100 km and mesoscale at 100–1000 km. The distance-ratio scale method developed by Navarro (2010) can be used as a direct measurement of the scale at which an animal operates in its environment.

The aim of this study was to investigate the foraging behaviour of the breeding African penguins around Dyer Island. I investigated the foraging areas and diving behaviour of breeding African penguins and consider inter-annual differences. Given the assumption that the availability of food plays a primary role in breeding success and ultimately population trends, I hypothesized that the African penguins at Dyer Island are foraging at greater distances, having longer foraging trip durations and lower dive and foraging efficiencies than that observed for penguins at other colonies. I also used the distance-ratio scale (DRS) approach devised by Navarro (2010) to investigate the scale at which the African penguins were foraging and to assess if this varied between years.

METHODS

Study Site

This study was conducted at Dyer Island (34'41'S 19'25'E) (Figure 1), off the south-west coast of South Africa (see Chapter 1). Dyer Island is currently the fifth largest breeding colony of African penguins in South Africa (Crawford *et al*. in press). The number of breeding pairs on the island declined from an estimated 22 655 pairs in 1979 (Shelton *et al*. 1984) to less than 2 000 pairs in 2010 (Crawford *et al*. in press, Chapter 1).

Data logger deployment

Birds were equipped with GPS-TD loggers (a global positioning system recorder, combined with a temperature-depth recorder) supplied by earth&OCEAN technologies, Kiel, Germany (Figure 2). These devices record the birds' position at sea, as well as their diving depth and the water temperature. Dive depth is obtained from water pressure and the water temperature *in situ* (Ludynia 2007). The loggers recorded latitude and longitude to an accuracy within 20m at time intervals of one minutes, and depth to the nearest 0.1m at intervals of one second (product information earth&OCEAN technologies and Ryan *et al.* 2004). The pressure and temperature sensors record water depth and temperature with an accuracy of 4mbar and 5mK, respectively (product information earth&OCEAN technologies). The GPS-TD loggers weighed 75g, including the battery, which is less than 2.5% of adult body weight, and the dimensions of the logger were 96×39×26.5mm (Ryan *et al.* 2004).

Loggers were deployed on breeding African penguins at Dyer Island during May, July and August 2008; May, July and August 2009, and May 2010. Prior to each session of deployment, 20 nests were marked and the sea-going rhythm of the chick-rearing adults was monitored for 2–3 days prior to the deployment of the loggers (Appendix 1 for 2010 example). Nests used were those that contained one or two chicks of small to medium downy size to maximise likelihood of retrieval of the device. One bird in each pair was marked on the neck with Porcimark®, an animal marker. The Porcimark® was sprayed onto the end of a 1m pole and the end placed on the neck of the bird and the Porcimark® rubbed onto the feathers. No birds were handled during the marking process. To test for disturbance and device effects, those nests not used to equip birds served as controls. The nests were subsequently checked three times daily (Appendix 1).

In 2008, nests were checked at 6:00, 9:00, 12:00, 18:00 and 21:00 to ascertain which parent (marked or unmarked) was on the nest and to determine at what time the birds returned from the sea, and when the partner in turn left for the sea. Nests were checked from a distance to minimise disturbance. In 2009 and 2010, nests were checked at approximately 6:00, 12:00 and 18:00.

Five GPS-TD loggers were available for this study. The method of logger deployment was the same as that described by Wilson *et al.* (1997), Ludynia (2007), Pichegru *et al.* (2010). All nests used were those within artificial burrows or within old buildings, and no open nests were studied. Birds were captured by hand at the nest site in the afternoon before the return of the partner. The loggers were attached to the birds' lower back to cause the least impact to the bird's hydrodymanics (Bannasch *et al.* 1994). Waterproof TESA® tape which causes no damage to the plumage (Wilson *et al.* 1997) was used to attach the logger (Figure 3). The bird was then returned to its nest (Figure 4). The total procedure took less than 10min.

The GPS loggers were programmed to get positional fixes every one, three or 30 minutes (settings varied between deployments) when the birds were at the colony or drifting on the surface and immediately after surfacing following each dive (Table 2). Both sensors were set to store data every second, allowing a detailed analysis of diving patterns and water temperature structure (Ludynia 2007). Nests sites of instrumented birds were monitored until the bird returned. On return to the nest, the logger was removed and the adult was re-weighed.

Data Analysis

Positional data were analysed using ArcView 3.1. The foraging range was the maximum distance to the colony (Wilson *et al.* 1989). Distance travelled was calculated by interpolating between positions. Trip duration was the time between departure from the colony and return to the nest. In order to estimate how directly a bird reached its foraging area, the loop factor was defined as the ratio of total distance travelled to the foraging range. The closer this value is to two, the more directly the bird swam to its foraging area (Ludynia 2007).

Dive data were analysed using the programme MT–Dive software (Jensen Software System), defining dives as equal to, or deeper than 3m (Tremblay and Cherel 2003).

Various criteria have been used to distinguish foraging dives from travelling dives, the criteria of which depending on the authors and species studied (Tremblay and Cherel 2003). Ludynia (2007) described foraging dives as all dives > 10m on the basis of a well-defined mode in the dive frequency distribution similar to that of previous studies (Ydenberg and Clark 1989, Luna Jorquera and Culik 1999, Tremblay and Cherel 2003). Pichegru *et al.* (2010) described feeding dives as those > 3m, both studies of which investigated foraging behaviour on African penguins. For comparative purposes, foraging dives in this study were defined as all dives > 10m following the convention by Ludynia (2007) and all other dives were considered travelling dives. Analyses were repeated for all dives > 3m and for dives > 10m to assess the difference. The numbers of foraging dives per hour were calculating according to the hours when diving activity was recorded. Hours during the day and night time hours, when no diving took place, were not included in this calculation. Trip duration, total distance travelled, foraging range, dive depth and duration and diving efficiency was calculated for each foraging trip in order to compare foraging effort between years, with year as the dependant variable using the Kruskall Wallis test.

Diving efficiency was defined as the ratio of bottom time duration and the sum of dive duration and post-dive surface time (Ydenberg and Clark 1989, Cherel *et al.* 1999, Tremblay and Cherel 2003). Higher values for dive efficiency suggest a higher food intake than lower values (Tremblay and Cherel 2003).

For each track for which complete dive data were available, dive efficiencies were not calculated for dives which had no bottom time. In addition, all dives which had a post-dive surface time exceeding 10min were deleted from the analysis because these pause times represented a long break in foraging unrelated to a physiological recovery after a dive.

Foraging efficiency was defined as the time spent diving as a percentage of the time spent at sea during the entire trip (Cherel *et el.* 1999, Ludynia 2007). I calculated the foraging efficiency for foraging dives greater than 10m. The vertical distance was calculated as the sum of all depths from each dive multiplied by two (Tremblay and Cherel 2003).

I used the distance-ratio scale (DRS) to obtain a measure of the scale at which an animal is operating (Navarro 2010). For each point along the track a circle is positioned that expands to include subsequent points along the track until the distance ratio, i.e. the actual distance covered divided by the radius, was greater than a pre-defined tolerance level. The radius for the point immediately before surpassing the given tolerance was considered the forward scale value (DRSf). Similarly, the calculations were repeated using preceding points along the track to obtain a backward scale value (DRSb); the DRS of the focal point is defined to be DRSf + DRSb. A tolerance value of 1.2 was used, as recommended by Navarro (2010).

Area restricted search (ARS) behaviour was equated to fine-scale movement, i.e. fixes with DRS < 1 000m. The fine-scale fixes were extracted from both complete and incomplete tracks; these were used to estimate kernel densities in a 0.00625° × 0.00625° grid (*ca*. 0.69×0.59km). Similarity or overlap in density distribution was evaluated with Morisita's index as modified by Horn (Ricklefs and Lau 1980), which varies between 0 (no overlap) and 1 (complete overlap). Kernel density maps were also produced for fixes corresponding to dives, and the similarity between dives densities and ARS densities were calculated using Morisita's index.

Statistical tests were performed using GENSTAT 12.1. The five point statistical description (including the mean) was calculated for all birds combined for one year. Kruskal Wallis test was performed to test differences between the three years. DRS analyses were done using program R (2.10.0, Windows version) (R Development Core Team 2009). The R-function *kde2d* in package *MASS* of Venables and Ripley (2002) was used to estimate Kernel densities.

RESULTS

In 2008, 16 logger deployments were made between 24 July and 28 August (Appendix 2). Of these, seven complete tracks were obtained and 1 track had GPS but no dive data. Reasons for incomplete data are provided in Appendix 2. In 2009, 23 birds were equipped with loggers between 27 May and 27 July, from which 15 tracks were obtained (Appendix 2). In 2010, 10 birds were equipped with loggers between 22 and 26 May (Appendix 2).

Device effects

All devices were retrieved during the course of the study, and no birds abandoned the nest except for one that was found later at Stony Point colony, c 60 km away from Dyer Island. Nest attendance patterns were similar on logger equipped individuals compared to that of control nests (Appendix 1). These data are insufficient for formal statistical analyses, but the visual appearance is of no impact on behaviour. All chicks in all nests monitored (including those of logger-equipped birds) survived and fledged (L. Waller unpubl. data).

Trip duration

Over the three-year study period, average trip durations were 28.15 h (n=8; range 12.0–35.7 h) in 2008, 35.07 hrs (n=15; range 10.5–83 h) in 2009, and 23.05 hrs (n=8; range 11–36 hrs) in 2010 (Table 1). These were not significantly different (Kruskal Wallis test, H=1.024, p=0.599).

Of the 35 trips overall, 11 were day trips, 24 were overnight trips, and there were overnight and day trips in each year (Appendix 3). In 2008, nine birds had an average departure time of 06:45, generally arriving back at the colony in the early evening, on average 17h53, which was about an hour before sunset (Appendix 3). Similarly, most birds left the colony in the early hours of the morning in 2009 (n=16; range 03:30–15:00) (Appendix 3). Average departure time in 2009 was 05:50, two hours before sunrise. Arrival time ranged from 16:25–20:15 (0.5 h before to 2.5 h after sunset). Average departure time in 2010 was 06:40 in 2010 (n=9; range 00:50–15:30) (Appendix 3), which was about one hour before sunrise. Arrival time ranged from 15:00 to 20:00 (between 2.8 h 50 before to 3.0 h after sunset (Appendix 3).

Foraging area

Over the course of the study, median foraging range was 38.2 km (n=11; range 19.0–45.6 km), 21.3 km (n=16; range 11.6–52.1 km) and 20.2 km (n=8; range 17.6–29.4 km) for 2008, 2009 and 2010 respectively (Table 1). Birds generally swam in a south westerly, southerly and southeasterly direction from Dyer Island in 2008 and 2009, and in a northwesterly direction into Walker Bay in 2010 (Figure 5). The median total distance travelled was 77.0 km (n=8; range 53.6–166.4 km), 77.1 km (n=15; range 34.4–315.5 km) and 75.7 km (n=8; range 27.1–126 km) for 2008, 2009 and 2010 respectively

(Table 1). Median loop factor was 2.58 (n=8; range 1.36–3.92), 2.98 (n=15; range 2.35–17.32) and 3.49 (n=8; range 1.46–4.39) for 2008, 2009 and 2010 respectively (Table 1).

Foraging range was significantly related to trip duration in 2008 ($r=0.968$; $p<0.001$; n=8), 2009 ($r=0.598$; $p=0.018$; n=15) and 2010 ($r=0.789$; $p=0.0199$; n=8) (Figure 6). Total distance travelled was not significantly related to trip duration in 2008 ($r=0.546$; $p=0.1618$) but was in 2009 ($r=0.759$; $p=0.001$; n=15) and 2010 ($r=0.926$; $p<0.001$; n=8). No significant relationship between total distance travelled and foraging range was found in 2008 ($r=0.517$; $p=0.189$); the relationship was significant in 2009 ($r=0.638$, $p=0.010$) and 2010 ($r=0.756$, $p=0.030$).

Birds on day trips had foraging ranges of 19.0 km each, 15.3 km (range 11.6–19.8 km) and 18.9 km (range 17.6–20.7 km) in 2008, 2009 and 2010 respectively (Appendix 3). Overnight trip foraging ranges averaged 38.9 km in 2008 (range 27.3–45.6 km), 31.4 km (range 12.0–52.1 km) in 2009 and 24.82 km (range 19.7–29.4 km) in 2010 (Appendix 3). Total distance travelled on day trips was 53.6 and 54.0 km in 2008, an average of 46.3 km (range 34.4–56.2 km) in 2009 and 47.5 km on average (range 27.2–66.9 km) in 2010 (Appendix 3). For overnight trips, average total distance was 92.9 km in 2008 (range 58.4–166.4 km), 151.4 km (range 85.7–315.6 km) in 2009 and 99.1 km (range 84.5–126.4 km) in 2010 (Appendix 3).

There were no significant differences between foraging range ($H=4.59$, $p=0.101$), total distance travelled ($H=0.8551$, $p=0.652$) and loop factor ($H=3.71$, $p=0.156$) between the three years (Kruskal Wallis tests).

Diving summary

Dive analyses were performed on complete foraging trips. For 2008, 2009 and 2010, 3313, 4925 and 3215 dives deeper than 3 m were recorded respectively (Table 1). Dives between 3 m and 10 m were travelling dives and those greater than 10 m, were foraging dives (Figure 7 and 8). Totals of 2149, 3695 and 2295 foraging dives were recorded in 2008, 2009 and 2010, representing 64.8%, 75.0% and 71.4% of the total diving activity respectively (Table 1).

Median dives per trip

Median number of foraging dives per trip was 295 (n=7; range 89–535), 421 (n=9; range 125–818) and 323 (n=7; range 210–456) for 2008, 2009 and 2010 respectively (Table 1). For day trips, the number of foraging dives per trip was 89 and 176 in 2008 (n=2), 181, 195 and 125 in 2009 (n=3) and a median of 236.5 in 2010 (n=4, range 210–323) (Tables 2, 3, 4, Appendix 4, 5, 6). For overnight trips, median number of dives was 317 (n=5; range=280–535) in 2008, 501 in 2009 (n=6; range=420–818) and 454 in 2010 (n=3; range=379–456) (Tables 2, 3, 4, Appendix 4, 5, 6).

Foraging dives per hour

Foraging dives per hour for day trips was 8.9 and 19.6 in 2008, 18.1, 19.5 and 15.6 in 2009 and 24.9 (range=21–32.3) in 2010 (Table 2,3,4, Appendix 4,5,6). For overnight trips, median dives per hour was 18.7 (n=5; range=13.4–24.3) in 2008, 21.0 (n=6; range=15.6–27.4) in 2009 and 23.9 (n=3; range=22.8–25.3) in 2010 (Tables 2, 3, 4, Appendices 4, 5, 6).

Time of diving

Almost all diving activity took place between 06:15 and 18:30 (Figure 9), with most taking place between 08:00 and 18:00 (Figure 10). For foraging dives (> 10 m), peak diving activity occurred between 14:00 and 16:00 in 2008, 08:00–12:00 in 2009 and 12:00 and 14:00 in 2010 (Figure 10). For the birds on day trips, foraging diving generally stopped earlier than the birds on overnight trips, the sample sizes being too small for further analyses (Table 3,4,5 and Appendix 4).

Maximum depth

The median maximum dive depth (of the maximum depth recorded for each trip) was lower in 2010 than that in 2008 and 2009 with 63.0 m (n=7; range 49.5–76.6 m), 59.54 m (n=9; range 46.8–78.2 m) and 51.9 m (n=7; range 27.8–68.9 m) recorded for all birds in 2008, 2009 and 2010 respectively (Table 1). Median dive depth for all dives deeper than 3 m was 13.6 m (mean of all dives=17.95; n=7 birds and 3313 dives) in 2008, 17.55 m (range 3.0–78.19 m) in 2009 and 14.03 m (mean of all dives=17.27; n=7 birds and 3215 dives) in 2010 (Table 1). Median depth for foraging dives was 20.9 m (mean of all foraging dives: 24.3 m; n=7 birds and 2149 dives) in 2008, 22.5 m (range 10.0–78.2 m) in 2009 and 17.4 m (range 10.0–68.9 m) in 2010 (Table 1). The deepest dives took place between 10:00–12:00 and 18:00–20:00 in 2008, 16:00–18:00 in 2009 and 11:00 and 12:00

in 2010 (Figure 11). The mean vertical distance travelled 16.99 km (n=7; range 5.2-30.6 km), 22.4 km (n=9; range 8.9-38.8 km) and 15.9 km (n=7; range 10.4-26.2 km) for 2008, 2009 and 2010 respectively (Table 1).

Dive duration

Median dive duration for all dives deeper than 3 m was 57 s (range 5–138 s) in 2008, 63 s (range 5–168 s) in 2009 and 55 s (range 6–120 s) in 2010 (Table 1). For foraging dives, median dive duration was 68 s (range 14–138 s), 72 s (range 16–168 s) and 61 s (range 12–120 s) for 2008, 2009 and 2010 respectively (Table 1). The average bottom time for all dives in 2008 was 25 s (n=3313, range 0–80 s), 28 s in 2009 (n=4925, range 0–87 s) and 32 s (n=3215, range 0–77 s) in 2010 (Table 1). For foraging dives, the average bottom time was 29 s (n=2149, range 0–80 s) in 2008, 31 s (n=3695, range 0–87 s) in 2009 and 35 s (range 0–77 s) in 2010 (Table 1). Dive duration was significantly correlated with dive depth in 2008 ($r=0.789$, $p<0.001$), 2009 ($r=0.800$, $p<0.001$) and 2010 ($r=0.758$, $p<0.001$) (Figure 12). Bottom time duration was significantly related to dive depth in 2008 ($r=0.166$, $p<0.001$) and 2010 ($r=0.421$, $p<0.001$), but not for 2009 ($r=0.007$, $p=0.6701$).

After removing post-dive pauses exceeding 10 minutes, post-dive pause was significantly related to dive depth in 2008 ($r=0.254$, $p<0.001$), 2009 ($r=0.235$, $p<0.001$) and 2010 ($r=0.197$, $p<0.001$). Dive duration was significantly related to post-dive pause in 2008 ($r=0.191$, $p<0.001$), 2009 ($r=0.172$, $p<0.001$) and 2010 ($r=0.138$, $p<0.001$). Number of foraging dives per hour, mean dive depth, mean foraging dive depth, mean bottom time duration, mean foraging bottom time duration and mean foraging dive duration were significantly different between years (Table 5).

Diving and foraging efficiency

Mean diving efficiency for foraging dives for all years was 0.40 (2008 range 0–0.77; 2009 range 0–0.69 and 2010 range 0–0.73) (Table 1) and was not statistically different between years ($p=0.742$). Diving efficiency for all foraging dives was significantly related to dive depth in 2008 ($r=0.413$, $p<0.001$), 2009 ($r=0.300$, $p<0.001$) and 2010 ($r=0.252$, $p<0.001$) (Figure 13). Diving efficiency tended to decrease with increasing depth.

In 2008, birds spent on average 20.8% of their time at sea foraging, i.e diving to a depth greater than 10 m (n=7, range 12.7–28.7%) (Table1). In 2009, foraging efficiency (foraging dives) was on average 24.8% (n=9, range 17.4–33.7%). Birds in 2010 spent on average, 27.4% of their time at sea foraging (n=7, range=21.6–35.0%). Foraging efficiency differed significantly between years (p=0.037) (Table 5).

Distance-ratio-scale (DRS)

DRS values across all tracks were summarised in Figure 14 using a log-binning method (LBN) and the frequencies were normalized according to the bin width. The largest normalized frequencies were for the 33–64 m and 65–128 m bins. DRS values < 1024 m are the dominant feature with 90.9% of the normalised frequencies within fine scale range (1–1000 m). As the DRS values increased, the frequency of the movements in these bins decreased, with 10% of the values in the coarse scale (1–100 km).

Time-space analysis of fine-scale movement

Variability between breeding seasons in the distribution of fine-scale movement, i.e. fixes with DRS < 1000 m, is shown in Figure 15. The kernel density distribution showed overlap between the 2008 and 2009 breeding season (28.9%), but not between 2008 and 2010 (0.6%) and 2009 and 2010 (1.5%).

Variability between breeding seasons in the dive positions of African penguins is shown in Figure 15. Overlap between seasons was greatest between 2008 and 2009 (75.6%), with little overlap between 2008 and 2010 (14.4%) and 2009 and 2010 (14.9%). Comparisons of the kernel density estimations of fine-scale DRS and dive positions show a spatial disparity for all years. Overlap measured with Morisita's Index as modified by Horn (Ricklefs and Lau 1980) between fine–scale DRS and dive densities were 38.0, 52.0 and 31.8% for 2008, 2009 and 2010 respectively (Figure 15).

DISCUSSION

Device effects

The impacts of deploying recording devices on penguin behaviour at sea has been demonstrated in a number of studies (e.g. Wilson *et al*. 1986a, Bannasch *et al*. 1994, Culik *et al*. 1994, Wilson *et al*. 2004). Previous studies using the same devices showed no significant difference in the foraging behaviour of birds equipped with devices and

control birds (Petersen *et al.* 2006, Ludynia 2007, Pichegru *et al.* 2010), and the devices are 2.5% of the penguins' adult body weight (Ryan *et al.* 2004). In this study logger-equipped birds had a similar foraging behaviour to that observed prior to deployment (Appendix 1).

Trip duration

Penguins from Dyer Island had longer trip duration, foraging ranges and travelled longer distances than birds in most other studies of African penguins (Tables 6 and 7). During this study, most tracks were obtained from birds that stayed at sea overnight, incomplete tracks due to limited battery life also represented overnight trips. This is unlike what is found in studies of African penguins at other South African colonies. For instance, mean trip duration for Dyer Island was 58% longer than that found at Boulders, Dassen Island and Robben Island in 2003 (Petersen *et al.* 2006, Ryan *et al.* 2007), and c. 45% longer at St Croix Island and Bird Island in 2008 and 2009 (Pichegru *et al.* 2010) (Table 6). Mean trip duration of penguins at St Croix in Algoa Bay in 1984 and 1985 (Heath and Randall 1989) however, was longer by c. 24% than penguins from Dyer Island (Table 6).

From February, anchovies recruit into the fishing region off the west coast of South Africa, migrating southwards in dense shoals by day, and in diffuse aggregations at night (Hampton 1987). This area is a productive fishing ground (Crawford *et al.* 1987), and it is likely that the abundance of fish in the west coast area is the reason for the shorter trip durations and foraging ranges of African penguin on the west coast.

Trip duration at Dyer Island was three times longer than that found for birds from Mercury Island, Namibia (Table 6). Most (e.g. 12 of 13 birds in 2005) Mercury Island breeding penguins made day trips (Ludynia 2007), unlike that at Dyer Island where 23 of 34 trips of the trips were overnight trips. The shorter trip duration of birds at Mercury Island, Namibia, suggests that feeding conditions are better for African penguins in Namibia compared to that in the South African colonies. Ludynia *et al.* (2010) however, discovered that the low energy content of the bearded goby *Sufflogobius bibarbatus*, the primary prey item of African penguins in Namibia since the decline of the sardine stocks in the 1970s, is the limiting factor in those penguin colonies. The bearded goby has lower energy content than sardine, so the penguins have to work harder to survive and provision for their chicks. Ludynia *et al.* (submitted) concluded

that low prey quality rather than abundance is driving population dynamics of African penguins and other top marine predators in the northern Benguela and while the foraging tracks suggested goby is more abundant than prey in South Africa as indicated by the shorter foraging trips, it is not as nutritionally beneficial and so it is important to consider other aspects such as diet when making broad, regional comparisons of foraging behaviour in seabirds.

Wilson (1995) showed that the distance travelled during each foraging trip was related to time spent by the birds at sea. Similar results were found in this study, as has been found in other studies on African penguins (Petersen *et al*, 2006, Ludynia 2007). The same result has been observed in Humboldt penguins *Spheniscus humboldti*; daily distance travelled were correlated to time spent at sea, with a mean distance travelled of 26.5 km (Luna-Jorquera and Culik 1999), which is 69% lower than that found for African penguins on Dyer Island.

Trip duration is hypothesed to indicate local food availability and abundance (Petersen *et al*. 2006). Shorter foraging trips are thus likely to be indicative of good local feeding conditions. Foraging trip duration for a breeding African penguin is time constrained because the adult needs to return to the colony to feed its chick and relieve its mate. The shorter the trip duration, the more frequently the adult is able to feed its chick; thus short trips would presumably lead to fast growing chicks in good condition with short fledging periods. Shorter foraging trips are also less energetically expensive for the adult than longer ones. Turn-around periods for incubating and guarding adults which have shorter foraging trips would presumably be advantageous, promoting good breeding condition throughout the breeding season resulting in chicks which fledge in the minimum fledging period. This would give the adult additional time to develop good condition prior to moult, leading to a rapid recovery of condition after moult in preparation for the next breeding season. Results of this foraging study suggest the hypothesis that chick condition on Dyer Island would be lower than on islands where the adults had shorter foraging trips. This is indeed what has been found (Chapter 4).

Similarly to that reported for African penguins in other studies (Frost et al. 1976, Wilson 1985a, Wilson *et al.* 1988, Wilson and Wilson 1990, Culik *et al.* 1988, Otley *et al.* 2004, Petersen *et al.* 2006, Ludynia 2007, Ryan *et al.* 2007), birds in this study generally left on foraging trips early in the morning, foraged during the day and returned in the

evening. However, unlike Namibian birds which on overnight trips would leave in the late afternoon or early evening (Ludynia 2007), Dyer Island penguins during the course of this study on overnight trips left in the early morning, similar to that of birds which went out on day trips. There was only one bird in each year that had an overnight trip that left in the afternoon. This is in contrast to the Namibian birds, which mostly left late (presumably because the partner returned late) and thus only had one complete day at sea (Ludynia 2007). In a study on African penguins from St Croix Island in 1984 and 1985 however, 23 of the 25 penguins tracked left in the evening (Heath and Randall 1989).

This suggests that at Dyer Island, birds that go to sea early on the first day do not obtain enough food to return to feed their chicks, and thus stay out another day (Ludynia 2007). Although African penguins rarely forage in groups exceeding 10 individuals (Duffy 1983, Wilson *et al*. 1986), there are advantages in leaving the colony when most other birds are doing so. African penguins commuting between their breeding colony and fishing area have been reported forming groups of up to 60 individuals (Wilson and Wilson 1990). Dyer Island is one of the seabird breeding colonies in the southern Benguela Upwelling Ecosystem that is considered to be significantly impacted by predation by Cape fur seals *Arctocephalus pusillus pusillus* (Makhado 2009, CapeNature unpubl data). It is also an area where great white sharks *Carcharodon carcharias* have been observed killing seabirds (Johnson *et al*. 2006). Reducing this risk could play a role in determining the foraging behaviour, and departure and arrival times of foraging African penguins (Randall *et al*. 1988). In some areas, extended foraging trips may also increase the risk of mortality through predation, and so there is a survival advantage to shorter foraging trips. Dyer Island penguins, with longer trip duration than penguins at other colonies may be trading off the increased risk of predation at sea, with minimising predation with timing arrival to reduce predation closer to the colony. What is not known is the degree of predation of seabirds by seals farther out at sea that is not visible from observation points on the island. There is evidence of this occurring with adult Cape gannets *Morus capensis* carcasses being found along Die Plaat, the section of coastline adjacent to the Walker Bay Nature Reserve (CapeNature unpubl data). This area is approximately c. 400 km from Lambert's Bay and c. 250 km from Malgas Island, both of which are Cape Gannet breeding colonies where these birds would likely have originated from. A joint penguin and seal and shark GPS tracking programme around Dyer Island would provide useful

insights into further understanding the marine predator and prey dynamics around the island.

Foraging area

Penguins are not adapted to feed on spatially or temporally unpredictable food sources, because swimming renders the foraging area available to them much smaller than that of flying seabirds which are able to search for unpredictable patches over larger areas (Wilson 1985a, Tremblay and Cherel 2003). Being central place foragers, the short feeding range of breeding African penguin requires a predictable prey distribution (Frost *et al.* 1976), that of anchovy and sardine, their primary prey species (Rand 1960, Furness and Cooper 1982, Wilson 1985b). African penguin diet samples carried out during the course of this study confirm the dominance of these two prey species, specifically anchovy (Crawford *et al.* in press). This could be achieved through either encountering single, large spatially predictable prey patches, or many small prey patches that are encountered frequently (Wilson 1985b). If birds were primarily feeding on large predictable shoals, one would expect birds to travel similar distances in a foraging trip, and the converse for smaller, spatially unpredictable schools (Wilson 1985b). The foraging area for birds sampled from Dyer Island during 2008 was similar for all birds, with birds tending to travel south and south west of the colony. This primary foraging area did not differ between 2008 and 2009, although during 2010, however, birds foraged predominantly within the Walker Bay area, with no birds heading out in a south and south westerly direction as they did in the two years previously. The school sizes of anchovy and sardine are highly variable. Anchovy can occur in large schools of many tons of fish and in small widely scattered schools (Shelton and Hutchings 1981). Wilson (1985a) found a positive correlation between distance travelled and amount of food ingested, which was said to be indicative of penguins feeding on small schools of randomly distributed prey where there was numerous prey encounters. Small schools are likely to be encountered more often under conditions of random search and thus are a spatially predictable food source which can be exploited by the penguin within its limited foraging range (Wilson 1985a).

The Benguela Upwelling Ecosystem is highly variable (Field and Shillington 2004, van der Lingen et al. 2006), and while the route of recruit migration is known at a large scale, these resources are less predictable and patchily distributed in the ocean at a smaller scale. One could then expect annual variability in foraging areas for marine top

predators. Much attention has been given to the establishment of Marine Protected Areas (MPAs) to protect threatened top predators, with some of these studies basing recommendations on foraging behaviour of the species it aims to protect (Pichegru *et al.* 2010, Ludynia *et al.* submitted). An MPA boundary was proposed along the Namibian coastline, based on foraging data from two seasons from African penguins and Cape gannets (Ludynia 2007). A further three-year data set was able to confirm those boundaries because the foraging tracks were similar (Ludynia *et al.* submitted). Results in this study suggest how variable foraging behaviour could be, even within the same species, because an MPA declared around Dyer Island based on the 2008 and 2009 data, would not have allowed for annual variability in prey availability.

Ludynia *et al.* (2010) found that the primary prey item of Namibian African penguins was the bearded goby. Thus their foraging behaviour is determined by feeding on a stationary prey species that is possibly more reliable than the variable pelagic prey species that dominate the southern Benguela Upwelling Ecosystem. Certainly long term foraging datasets are required in order to fully understand the penguin foraging behaviour within the marine environment in which it operates.

Steinfurth (2007) found a coast-hugging foraging behaviour in the Galapagos penguin *Spheniscus mendiculus*; the birds did not forage more than 1 km from the shore, travelling parallel with the coast, with a mean maximum distance of 5.2 km. Trip duration was on average 8.4 h with penguins leaving between 05:00 and 06:00 and returning between 11:00 and 17:00. All of these parameters are substantially less than what was found for the African penguin at Dyer Island. Both species, like all Spheniscids are reliant on pelagic school fish such as anchovies and sardines (Wilson and Wilson 1995), species typical of upwelling ecosystems, yet no other *Spheniscus* species displays this coast hugging behaviour (Steinfurth 2007). Steinfurth (2007) argued that it may be factors other than food distribution that are limiting the range and population growth of the Galapagos penguin.

Diving behaviour

Time of diving

All diving activity was recorded during the daylight hours (Figure 9). This was an expected result, because African penguins rely on daylight to see and catch their prey (Wilson 1985a, 1985b, Wilson and Wilson 1995). Similar findings were found for African

penguins by Petersen *et al*. (2006), Ludynia (2007), Ryan *et al.* (2007). This was true both for all dives >3 m and for foraging dives >10 m.

In 2008, a bimodal peak when deepest dives were observed occurred between 10:00–12:00 and 18:00–20:00. In 2009 the deepest dives were observed between 16:00–18:00 and in 2010 the deepest dives were observed between 18:00–20:00. This was unlike the pattern observed in at Mercury Island, where the deepest dives took place around midday. Dyer Island birds had more overnight trips than Mercury Island birds, which could result in Dyer Island displaying diving activity in the late evening when birds on overnight trips could still be feeding. Luna-Jorquera and Culik (1999) found that Humboldt penguins also dive at night, reaching depths of 12 m, although there was uncertainty as to whether foraging continued at night. During the night, anchovies rise to the surface, but there has been little evidence to suggest there is ingestion (Wilson *et al*. 1993). See however DRS discussion below.

Dive depths

Luna-Jorquera and Culik (1999) stated that dive behaviour can be adjusted to that of their prey, and that Humboldt penguins (feeding primarily on anchovy) would not dive deeper than 50 m. Generally, the dive depth pattern did not differ between the years of this study (Figure 6). The main difference was in 2010, when a higher proportion of dives were made at the 5–10 m, 10–15 m and 15–20 m intervals than that of the previous years. Maximum dive depths reached by foraging penguins at Dyer Island fall within the range of that observed by other studies, and there were no significant differences between years. Mean maximum dive depths ranged between 61 m in 2008 and 2009 and 49 m in 2010; maximum depths of 77 m, 78 m and 69 m were recorded in 2008, 2009 and 2010 respectively. This is slightly deeper than that found by Peterson *et al*. (2006), although less than the maximum of 130 m observed by Wilson (1985a) using a capillary depth guage at Malgas Island; most birds at Malgas Island did not dive deeper than 30 m.

In 2010, unlike the two previous years, most of the foraging took place within the Walker Bay area, within an average depth of 50 m. This differs from 2008 and 2009, where most the foraging took place within an area of 65 m average depth. This indicates, similar to that found by Ludynia (2007), that the bathymetry of the areas around the breeding colonies influences diving behaviour, and a direct comparison of

diving depth between colonies as an indicator as to how hard the birds are working (and thus indicator of food abundance), may not necessarily be related to food abundance, but to the bathymetry of the surrounding area. Dive depth is also likely linked to prey distribution in the water column. There was a disparity in spatial overlap of dive positions and DRS fixes for all years, the highest of which was observed in 2010 when the birds were foraging predominantly in Walker Bay. The implication of this may be that the birds are foraging at a lower depth than that which is recorded as a dive in this study, i.e. dives occur at a depth < 3 m. Steinfurth (2007) found a mean dive depth of 3 m during a study of Galapagos penguins, and 90% of the time spent diving occurred at depths less than 8.5 m for males and less than 4.0 m for females. Both African penguins and Galapagos penguins feed on pelagic school fish such anchovy and sardine (Wilson 1995), and it is possible that African penguins at Dyer Island feed in shallow waters. Future studies need to examine the bathymetry around African penguin breeding colonies, and determine the volume of water available to them to forage, and assess how differences in the surrounding bathymetry is reflected in the diving behaviour.

Vertical distance

Mean total vertical distance travelled was higher at Dyer Island in all years compared to that recorded at Mercury Island (Table 6). Total vertical distance travelled can be used as an indicator of foraging effort (Cherel et al. 1999, Tremblay and Cherel 2003). These results suggest that Dyer Island penguins expend a higher foraging effort than those in Namibia. Penguins can dive deeply, increasing the volume of sea available to them in proximity to their breeding site compared with that of available to other seabirds (Wilson 1985a).

Various criteria have been used to distinguish foraging dives from travelling dives, the criteria of which depended on the authors and species studied (Tremblay and Cherel 2003). There may even be regional differences within species. The challenge in comparing other dive parameters in previous African penguin studies, such as number of foraging dives per trip, dives per hour for foraging dives, foraging dive duration, foraging bottom time, dive efficiency and foraging efficiency is that many of the studies have used a different depth delineation to describe foraging and travelling dives. Ludynia (2007) defined travelling dives as those from 3–10 m, and foraging dives > 10 m for a study on African penguin foraging in Namibia. This was based on a well-defined mode in the dive frequency distribution. Other studies analysed their dives as those ≤ 2

m as travelling dives and all subsequent analyses were done on dives ≥ 3 m (Ydenberg and Clark 1989, Luna Jorquera and Culik 1999, Tremblay and Cherel 2003, Peterson *et al*. 2006). Pichegru e*t al*. (2010) defined feeding dives as all dives greater than 3 m. Analyses in this study were performed using a split of all dives (those ≥ 3 m) and foraging dives (those ≥ 10 m). In that way, the most comparisons could be made.

In all years, dive frequency was highest between 5 and 15 m at Dyer Island and steadily decreased from then on (Figure 7). This was unlike that found at Mercury Island, where most diving took place from 3 to 10 m (Ludynia 2007). For the remaining dive depths, a similar dive depth frequency pattern was observed between the Dyer Island and Mercury Island birds (Ludynia 2007). Small scale fish surveys may be conducted around Dyer Island in 2011 as part of Oceans and Coasts Island Closure feasibility studies. The foraging data collected in this study and the depths at which the birds are diving will be useful data to compare the fish distribution data obtained from these surveys.

Dive duration

Average dive duration in this study (range 55−61 s) was similar to that observed by Ryan *et al*. (2007) for Boulders (mean 51.7 s; range 41−62 s) and Robben Island (50.7 s, range 39−68 s) (for dives ≥ 2 m), although less than that observed by Pichegru *et al*. (2010) in the Eastern Cape (range 72 s−80 s) over a similar time period for dives ≥ 3 m (Table 7). Median values for Dyer Island dive duration for the same depth at Mercury Island in 2005 and 2006 (42 s and 55s) were similar (Table 7). Foraging dive duration, those dives ≥ 10 m, was lower than that for birds at Mercury Island. Wilson (1985a) stated that penguins do not forage during short dives of 22 s, indicating birds are travelling rather than foraging. Similar patterns were found for mean bottom time for dives ≥ 2m at Boulders (26 s), Robben Island (25 s) and Dyer Island for dives ≥ 3 m (25 s, 28 s and 32 s for the three years). For the same dive depth, bottom time was shorter at Mercury Island in 2005 (12 s) and 2006 (16 s) (Table 7). Additionally, for dives ≥ 10 m the median bottom times in 2005 (24.0 s) and 2006 (29.0 s) for birds at Mercury Island, was shorter than that found at Dyer Island 36 s, 38 s and 29 s in 2008, 2009 and 2010 respectively. Dive duration and bottom time could be different due to difference in prey behaviour, such as stationary goby compared to that of pelagic anchovy and sardine which have faster swimming speeds, requiring longer pursuit diving than that of birds feeding on goby.

Diving efficiency and foraging efficiency

Both diving efficiency and foraging efficiency can provide an indication of prey availability and of the efficiency of the penguins in capturing the prey (Ludynia 2007). Diving efficiency for foraging dives was similar during the three-year study period, suggesting feeding conditions were similar. Additionally, overall median diving efficiency of foraging dives at Dyer Island was 0.41 over three years, more than twice as large as that obtained by Ludynia (2007) at Mercury Island, 0.18 over two years. This suggests penguins are able to find food more efficiently at Dyer Island than those at Mercury Island. When looking at the foraging efficiency however, Dyer Island birds spent on average 20.8%, 24.8% and 27.4% of their time at sea foraging in 2008, 2009 and 2010 respectively, which was lower to that of 30.6% and 29.5% for birds at Mercury Island in 2005 and 2006 (Ludynia 2007). Foraging time at sea at Dyer Island was also lower than that of Boulders in 2003 (47.7%) and Robben and Dassen Islands combined (42.9%) in 2003 (Petersen *et al.* 2006). With Dyer Island birds having a longer trip duration, travelling further and having more overnight trips than what has generally been recorded elsewhere, a lower foraging efficiency may indicate that are unable to locate/find food and so spend more time travelling to search for suitable prey patches. That Mercury Island birds travelled to the same foraging areas in both study years; in contrast the foraging areas of bird from Dyer Island varied substantially over the three years. Although sample sizes are small, this suggests that Dyer Island penguins spend more time searching for prey than Mercury Island penguins. The impact of this reduced foraging efficiency at Dyer Island carries over into chick growth rate and condition for the same period. Sherley (2010) found that Dyer Island African penguin chicks had, on average, a slower growth rates than chicks at Dassen Island, Robben Island, St Croix Island and Bird Island during 2008 and 2009. Chapter 4 demonstrated that chick condition at Dyer Island was consistently poorer at Dyer Island than at these other colonies during the same period.

The search strategy of African penguins at Dyer Island, indicated by the DRS analysis showed that most movement took place at the fine scale (1–1000m), which is what one could expect from a flightless bird. The frequency distribution of DRS fixes for African penguins at Dyer Island, is similar to that what Navarro (2010) found for the Cape gannet, a flying seabird, able to cover much larger distances. In addition, significant differences were found in trip duration, distance and flight speed of foraging Cape Gannets between Ichaboe Island and Malgas Island, which Mullers and Navarro (2010)

attributed to poorer feeding conditions experienced by birds at Ichaboe Island. However, despite these differences, the search strategies revealed by DRS analysis were indistinguishable between birds from the two colonies (Navarro 2010).

Overall Comments

Understanding the foraging ecology for the African penguin is a key issue for the conservation of this species (Frost *et al*. 1976), especially if interactions with fisheries are to be understood (Luna-Jorquera and Culik 1999). It would seem that understanding foraging ecology at colony level is also of importance, because factors impacting foraging behaviour may be colony specific. This is especially true in understanding the impact that fisheries have for surrounding colonies. Results of this study suggest that African penguins at Dyer Island work harder for their food than African penguins at most other colonies. This is supported by having longer trip durations, larger foraging ranges, larger total distance travelled (Table 6) as well as by several dive parameters (Table 7). This is further supported by results in Chapter 4 which showed chicks from Dyer Island had a consistently poor condition than chicks from other African penguin breeding colonies in South Africa over the same period of time.

Small-scale surveys of fish distribution and abundance around colonies, timed to coincide with logger deployment, would be valuable in understanding foraging behaviour in relationship to dynamic and unpredictable food sources. Both logger deployment and fish surveys are however expensive. Research should also focus on whether monitoring of chick growth rate (Sherley 2010, Navarro 2011) and chick condition indices (Chapter 4) are more easily measured surrogate variables, able to provide insights into the quality and quantity of food available to adults foraging around breeding colonies.

Although Dyer Island lies along the same anchovy and sardine migration route to that of Dassen Island, Robben Island, and Boulders, food seems to be scarcest for the penguins breeding at Dyer Island. This could be due to fishing pressure, or related to other factors such as predation, where staying away longer from the island reduces the risk of being eaten by seals, or a combination of factors. The relationship of penguin foraging and diving behaviour in relation to simultaneous fishing activities surrounding the island also needs to be investigated further. The differences in foraging behaviour

may also not be completely explained by prey availability but also by other factors such as bathymetry. There is a need for ongoing foraging studies to understand the birds' response to a changing, dynamic environment.

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Table 1: Summary of foraging and diving parameters of GPS TD equipped African penguins from Dyer Island, South Africa, for 2008, 2009, 2010. LQ= lower quartile, UQ= upper quartile

	2008							2009							2010						
Foraging Parameter	n	min	LQ	median	mean	UQ	max	n	min	LQ	median	mean	UQ	max	n	min	LQ	median	mean	UQ	max
Trip duration (hrs)	8	12.00	22.50	34.33	28.15	35.12	35.67	15	10.50	13.75	33.67	35.07	36.37	83.00	8	11	12.79	22.33	23.05	32.85	36
Foraging range (km)	11	19.00	30.71	38.18	35.24	42.37	45.58	16	11.65	16.09	21.33	23.75	30.07	52.12	8	17.62	18.60	20.19	21.84	23.00	29.4
Distance travelled (km)	8	53.62	57.32	77.02	83.10	87.67	166.43	15	34.41	52.28	77.10	95.89	96.88	315.55	8	27.15	51.17	75.71	73.27	92.20	126
Loop factor	8	1.36	2.17	2.58	2.53	2.85	3.92	15	2.35	2.66	2.98	4.25	3.68	17.32	8	1.46	2.53	3.49	3.29	4.30	4.39
Total no. of dives ≥ 3 m	3313							4925							3215						
Total no. of dives ≥ 10 m	2149							3965							2295						
No. of dives >3 m per trip	7	163	343	465	473	587	826	9	196	284	600	547.22	691	975	7	344	373.5	449	459.29	528	619
Number of foraging dives (>10 m)per trip	7	89	228	295	307	387	535	9	125	195	421	410.56	509	818	7	210	236.5	323	327.86	416.5	456
No. dives per hour (for hours diving) (all dives)	7	20.22	24.31	25.40	26.06	27.59	33.04	9	23.8	26	28.2	28.17	30	32.9	7	29.5	30	31.3	34.41	37.35	45.4
No. dives per hour (for hours diving) (foraging dives)	7	8.90	15.05	18.67	17.94	21.81	24.32	9	15.6	19.5	21	21.22	21.1	27.4	7	21	23.35	24.8	25.01	25.15	32.3
Maximum dive depth (m) per trip	7	49.50	55.94	63.03	61.42	65.30	76.63	9	46.81	55.0	59.54	61.67	65.40	78.19	7	27.8	40.69	51.86	49.22	57.3	68.9
Overall dive depth (m)	3313	3.0	7.63	13.61	17.95	25.85	76.63	4925	3.0	10.0	17.55	20.49	28.91	78.19	3215	3.01	9.422	14.029	17.27	21.15	68.9
Foraging dive depth	2149	10.0	14.04	20.87	24.30	32.81	76.63	3695	10.0	15.34	22.46	25.06	32.79	78.19	2295	10	13.34	17.414	21.25	25.39	68.9
Overall dive duration (s)	3313	5	40	57	56	72	138	4925	5	43	63	61	80	168	3215	6	45	55	55.4	67	120
Foraging dive duration (s)	2149	14	57	68	67	79	138	3695	16	57	72	71	85	168	2295	12	51	61	61.69	72	120
Overall bottom time (s)	3313	0	0	29	25	40	80	4925	0	0	31	28	44	87	3215	0	26	33	32.01	40	77
Foraging bottom time (s)	2149	0	0	36	29	43	80	3695	0	12	38	31	47	87	2295	0	29	36	35.41	42	77
Dive efficiency (all dives)	2377	0.00	0.35	0.41	0.39	0.46	0.77	3644	0.00	0.35	0.41	0.39	0.46	0.69	3164	0.01	0.34	0.42	0.40	0.47	0.73
Dive efficiency (foraging dives)	1585	0.00	0.35	0.41	0.40	0.46	0.77	2770	0.00	0.36	0.41	0.40	0.46	0.69	2282	0.00	0.35	0.42	0.40	0.47	0.73
Foraging efficiency (%)	7	12.73	15.77	19.17	20.79	26.71	28.66	9	17.39	22.19	23.44	24.81	26.00	33.71	7	21.56	23.45	25.00	27.36	31.55	34.98
Vertical distance (km)	7	5.24	11.95	16.17	16.99	21.50	30.58	9	8.92	11.31	24.12	22.43	28.71	38.79	7	10.38	10.66	11.65	15.86	20.76	26.15

Table 2: Dive summary for African penguins equipped with GPS TD loggers in 2008 on Dyer Island, South Africa

			All Dives > 3m						Foraging Dives > 10m						
2008	Day/ Over-night trip	Total no. dives per trip	Tot no. dives per day		No. dives per hour at sea	No. dives per hr diving	No. dives per hr diving		Total no. dives per trip	Tot no. dives per day		No. dives per hour at sea	No. dives per hr diving	No. dives per hr diving	
			Day1	Day2			Day1	Day2		Day1	Day2			Day1	Day2
CP1	Day	163	*	*	13.04	13.58	*	*	89	*	*	7.12	8.9	*	*
GPS2	Overnight	404	146	258	15.64	25.25	29.2	23.45	280	111	169	10.84	18.67	22.2	16.9
E17	Overnight	826	377	449	23.16	33.04	31.42	34.54	535	234	301	15.00	24.32	21.27	27.4
CP6	Day	281	*	*	23.5	25.55	*	*	176	*	*	14.67	19.56	*	*
OldA10	Overnight	552	292	260	16	24	26.55	21.67	457	253	204	13.25	24.05	25.3	22.7
CP2	Overnight	622	305	317	18.2	28.27	27.73	28.82	317	117	200	9.28	16.68	14.63	18.2
F5	Overnight	465	129	336	13.1	20.22	10.75	30.55	295	77	218	8.31	13.41	7	19.8

Table 3: Dive summary for African penguins equipped with GPS TD loggers in 2009 on Dyer Island, South Africa

		All Dives > 3m											Foraging Dives > 10m									
	Day/ Over-night trip	Total no. dives per trip	Tot no. dives per day				No. dives per hour at sea	No. dives per hr diving	No. dives per hr diving				Total no. dives per trip	Tot no. dives per day				No. dives per hour at sea	No. dives per hr diving	No. dives per hr diving			
			Day1	Day2	Day3	Day4			Day1	Day2	Day3	Day4		Day1	Day2	Day3	Day4			Day1	Day2	Day3	Day4
CP7	Day	280	*	*	*	*	20.48	28	28	*	*	*	181	181	*	*	*	13.24	18.1	18.1	*	*	*
CEM48	Overnight	563	213	350	*	*	16.72	28.2	23.7	31.818	*	*	509	201	308	*	*	15.12	26.8	22.3	30.8	*	*
CEM28	Day	284	*	*	*	*	27.05	28.4	28.4	*	*	*	195	195	*	*	*	18.57	19.5	19.5	*	*	*
E10	Overnight	691	311	380	*	*	19.74	32.9	28.3	38	*	*	421	225	196			12.03	21.1	20.5	21.8	*	*
CP15	Day	196	*	*	*	*	16.68	24.5	24.5	*	*	*	125	125	*	*	*	10.64	15.6	15.6	*	*	*
CP4	Overnight	975	259	267	232	217	11.75	23.8	28.8	24.273	19.3	24.1	818	218	222	185	193	9.86	21	24.2	22.2	15.4	24.1
K4	Overnight	634	329	305	*	*	18.65	31.7	27.4	38.125	*	*	493	260	233	*	*	14.50	27.4	26	29.1	*	*
K20	Overnight	702	288	276	138	*	11.32	26	24	25.091	34.5		533	214	203	116		8.60	20.5	19.5	18.5	29	*
K37	Overnight	600	258	342	*	*	18.05	30	23.5	38	*	*	420	176	244	*	*	12.63	21	16	27.1	*	*

Table 4: Dive summary for African penguins equipped with GPS TD loggers in 2010 on Dyer Island, South Africa

			All Dives > 3m										Foraging Dives > 10m									
	Day/ Over-night trip	Total no. dives per trip	Tot no. dives per day				No. dives per hour at sea	No. dives per hr diving	No. dives per hr diving				Total no. dives per trip	Tot no. dives per day				No. dives per hour at sea	No. dives per hr diving	No. dives per hr diving			
			Day1	Day2	Day3	Day4	(trip duration)		Day1	Day2	Day3	Day4		Day1	Day2	Day3	Day4			Day1	Day2	Day3	Day4
OldB8	Day	400	400	*	*	*	36.36	40	40	*	*	*	248	248	*	*	*	22.55	24.8			*	*
CP8	Day	454	454	*	*	*	34.92	45.4	45.4	*	*	*	323	323	*	*	*	24.85	32.3			*	*
CP14	Day	347	347	*	*	*	28.51	34.7	34.7	*	*	*	225	225	*	*	*	18.49	25			*	*
CEM2	Day	344	344	*	*	*	19.85	31.3	31.3	*	*	*	210	210	*	*	*	12.12	21			*	*
LU1	Overnight	619	376	243	*	*	17.35	29.5	31.3	27	*	*	456	241	215	*	*	12.78	22.8	21.9	23.9	*	*
CEM28	Overnight	449	73	376	*	*	16.43	29.9	24.3	31.3	*	*	379	61	318	*	*	13.87	25.3	20.3	26.5	*	*
CEM48	Overnight	602	356	246	*	*	16.72	30.1	32.4	27.3	*	*	454	234	220	*	*	12.61	23.9	23.4	24.4	*	*

Table 5: Results of Kruskall Wallis tests to compare diving parameters on GPS TD equipped African penguins at Dyer Island in 2008, 2009, 2010

Dive Parameter	H	P
No. dives	0.8026	0.669
No. foraging dives	0.9317	0.628
No. foraging dives per hour	6.907	0.031
Max depth	3.509	0.173
Mean depth	6.573	0.037
Mean foraging depth	6.540	0.038
Mean dive duration	3.167	0.205
Total dive duration	0.7778	0.678
Mean bottom time duration	7.542	0.023
Mean foraging bottom time	6.606	0.037
Mean foraging duration	6.683	0.035
Total foraging duration	0.8026	0.669
Foraging efficiency	6.606	0.037
Dive efficiency	0.5776	0.742
Vertical distance	1.876	0.391

Table 6: Foraging area parameters of African penguins in Namibia and South Africa

	Trip duration				Distance travelled				Foraging range				Loop factor				Source
	N	median	mean	Range	n	median	mean	range	n	median	mean	Range	n	median	mean	range	
Mercury Island 2005	12	13.34	–	10.57–27.18	12	57	–	44.4–91.1	12	21.6	–	14.1–31.9	12	2.9	–	2.4–3.2	Ludynia 2007
Mercury Island 2006	11	15.12	–	9.56–25.27	12	60.8	–	47.0–78.4	12	20.9	–	16.6–26.6	12	2.9	–	2.4–3.5	Ludynia 2007
Possession Isand 2005	3	25.53	–	7.59–27.33	3	61	–	34.4–76.1	3	10.4	–	6.2–11.4	3	5.9	–	5.6–6.7	Ludynia 2007
Halifax Island 2006	3	6.45	–	3.29–12.12	3	17.7	–	11.6–35.7	3	5.5	–	5.3–13.2	3	2.7	–	2.2–3.2	Ludynia 2007
Boulders 2003	14-16	–	13.18	10.6–15.8	14-16	–	46.4	17–62	14-16	–	18.5	5.8–27.9	14-16	–	–	–	Petersen *et al*. 2006
Robben & Dassen 2003	11-14	–	10.28	7.7–13.3	11-14	–	33.2	20–44	11-14	–	9.4	5.7–16.8	11-14	–	–	–	Petersen *et al*. 2006
Dyer Island 2008	8	34.33	28.15	12–35.67	8	77.02	83.1	53.62–166.43	11	38.18	35.24	19–45.58	8	2.58	2.53	1.36–3.92	This study
Dyer Island 2009	15	33.67	35.07	10.5 – 83	15	77.1	95.89	34.41–315.55	16	21.33	23.75	11.65–52.12	15	2.98	4.25	2.35–17.32	This study
Dyer Island 2010	8	22.33	23.05	11 – 36	8	75.71	73.27	27.15–126	8	20.19	21.84	17.62–29.4	8	3.49	3.29	1.46–4.39	This study
St Croix Island 1984 St Croix Island 1985	18	–	22.5	13.9–47.8	18	–	69.3	25.9–152.3	18	–	32.3	18.7–44.5	–	–	–	–	Pichegru *et al*. 2010
St Croix Island 2009	14	–	17.1	7.8 – 23	14	–	50.2	11.2–77.5	14	–	19.7	4.7–30.7	–	–	–	–	Pichegru *et al*. 2010
Bird Island 2008	30	–	15.6	9.7 – 24	30	–	39.2	25.6–66.7	30	–	14.5	6.3–30.3	–	–	–	–	Pichegru *et al*. 2010
Bird Island 2009	29	–	18	7.2 – 30	29	–	41.5	10.9–59.8	29	–	14	4.1–24.8	–	–	–	–	Pichegru *et al*. 2010

Table 7: Diving parameters of African penguins in Namibia and South Africa

	Mean Dive Depth (m)					Mean Dive Duration (s)					Bottom Time (s)			Foraging efficiency (%)			Vertical distance (km)		
	n	median	mean	max	Range	n	medi	mean	max	Range	n	median	range	n	medi	range	n	median	range
Mercury Island 2005 (≥ 10 m)*	12	34.8	–	74.1	10–74.1	12	82	–	142	13–142	12	24.0	0–89	12	30.6	14.2–49.6	–	–	–
Mercury Island 2005 (≥ 3 m)*	12	7.0	–	74.1	3.0–74.1	12	42.0	–	142	4–142	12	12	0–89	12	–	–	12	10.9	5.0–20.1
Mercury Island 2006 (≥ 10 m)*	10	27.0	–	76.8	10.0–76.8	10	80	–	135	12–135	10	29.0	0–79	10	29.5	23.7–52.6		–	–
Mercury Island 2006 (≥ 3 m)*	10	10.0	–	76.8	3.0–76.8	1	55.0	–	135	5–135	10	16	0–79	10	–	–	10	11.5	8.0–18.3
Possession Island 2005 (≥ 10 m)*	3	–	17.4	20.0	14.4–20.0	3	–	55.2	57.0	52.5–57.0	3	23.7	19–27	3	34.9	28.4–47.3	–	–	–
Halifax Island 2006 (≥ 10 m)*	2	–	39.05	1.8	36.34–1.8	2	–	92.5	105.0	80.0–105.0	2	30.25	25–35.5	2	45.5	43.5–47.5	–	–	–
Possession Island 2005 (≥ 3 m)*	3	–	7.4	8.7	6.2–8.7	3	–	35.2	40.5	27.0–40.5	3	15	12–18	3	–	–	3	12.6	6.8–16.6
Halifax Island 2006 (≥ 3 m)*	2	–	10.0	14.5	5.4–14.5	2	–	39.5	53.0	26.0–53.0	2	14.5	14–15	2	–	–	2	5.2	3.4–7.0
Boulders 2003 (>2m)	19	–	16.7	21.5	10.9–21.5	19	–	51.7	–	41–62	19	26.0	17–33	19	–	–	19	–	–
Robben Island 2003**	10	–	17.8	–	12.1–25	10	–	50.7	–	39–68	10	25.3	18–35	10	–	–	10	–	–
Dassen Island 2003**	2	–	–	–	18.9–22.1	2	–	–	–	38–44	2	–	24–27	2	–	–	2	–	–
Dyer Island 2008 (≥ 10 m)***	8	20.87	24.3	76.63	10.0–76.63	8	57	56	138	5–138	8	36	0–80	8	19.1	12.7–28.6	8	–	–
Dyer Island 2009 (≥ 10 m)***	15	22.46	25.06	78.19	10.0–78.19	15	63	61	80	5–80	15	38	0–87	15	23.4	17.4–33.7	15	–	–
Dyer Island 2010 (≥ 10 m)***	8	17.4	21.3	68.9	10.0–68.9	8	55	55.4	120	6–120	8	36	0–77	8	25.0	21.6–35.0	8	–	–
Dyer Island 2008 (≥ 3 m)***	8	13.61	17.95	76.63	3.0–76.6	8	57	56	138	57	8	29	0–80	8	–	–	8	16.2	5.2–30.6
Dyer Island 2009 (≥ 3m)***	15	10.0	20.49	78.19	3.0–78.19	15	61	63	168	61	15	31	0–87	15	–	–	15	24.1	8.9–38.8
Dyer Island 2010 (≥ 3 m)***	8	9.4	17.3	68.9	3.0–68.9	8	55	55.4	120	55	8	33	0–87	8	–	–	8	11.7	10.4–26.2
St Croix Island 2008 (≥ 3 m)****	18	–	26.4	84.9	–	18	–	79.6	163	–	18	–	–	–	–	–	–	–	–
St Croix Island 2009 (≥ 3 m)****	14	–	23	76.7	–	14	–	72.5	153	–	14	–	–	–	–	–	–	–	–
Bird Island 2008 (≥ 3 m)****	30	–	25	77.2	–	30	–	75.3	154	–	30	–	–	–	–	–	–	–	–
Bird Island 2009 (≥ 3 m)****	29	–	26.8	91	–	29	–	76.1	275	–	29	–	–	–	–	–	–	–	–

* Ludynia (2007), ** Ryan *et al*. 2004, *** Chapter 5, **** Pichegru *et al*. 2010

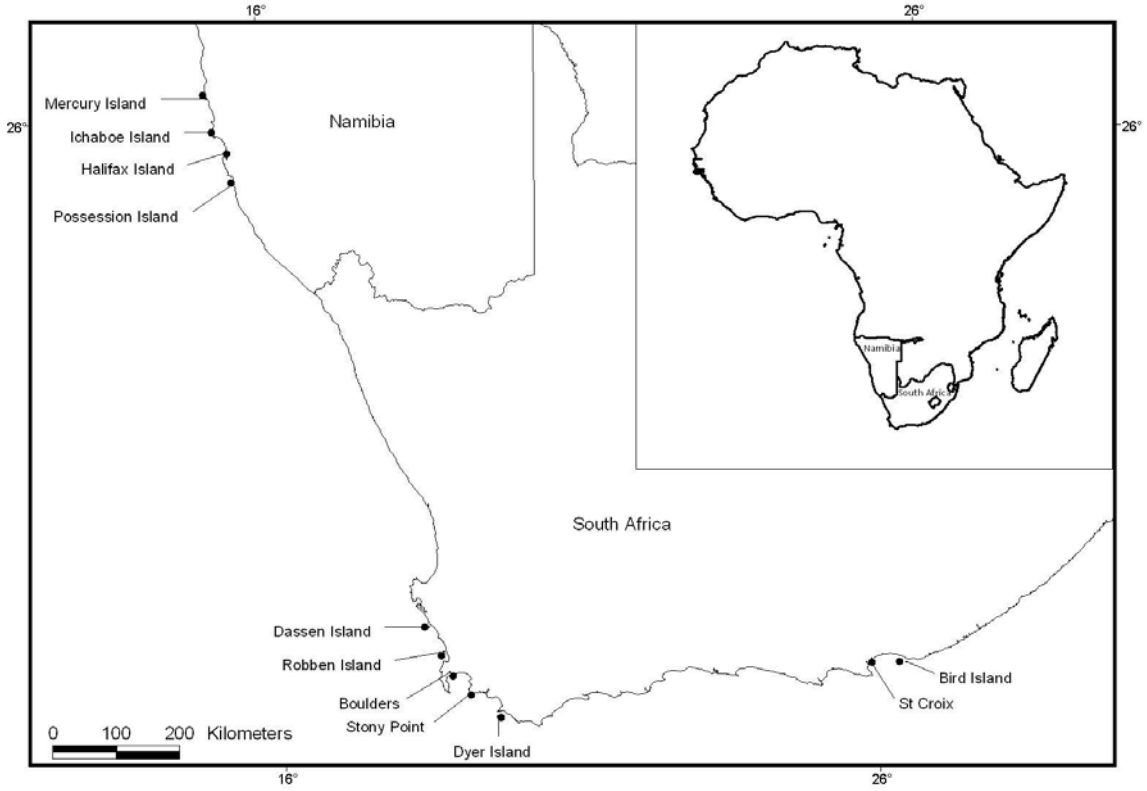

Figure 1: The south-west coast of Africa, indicating the location of African penguin breeding localities from Namibia and South Africa that are referred to in the text.

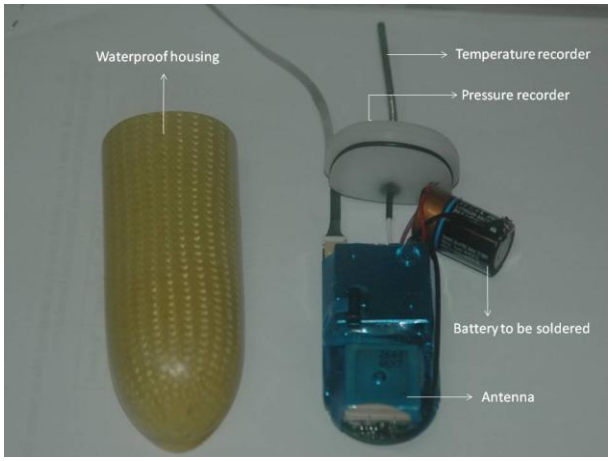

Figure 2: GPS TD loggers used on African penguins at Dyer Island, South Africa.

Figure 3: Deployment of GPS TD Loggers on African penguins at Dyer Island, South Africa.

Figure 4: GPS TD logger equipped bird at nest, prior to leaving for sea at Dyer Island, South Africa.

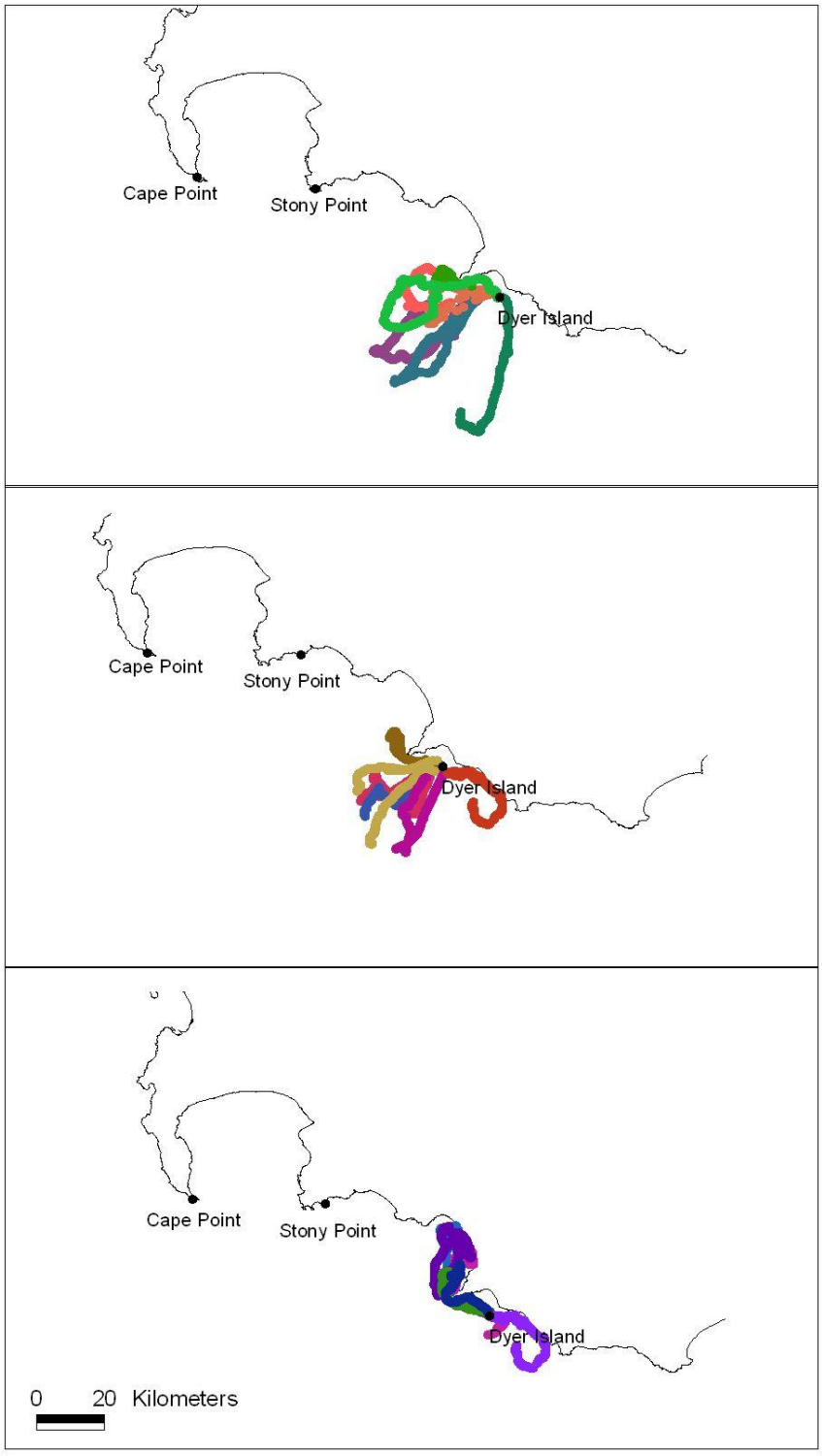

Figure 5: A sample of foraging tracks of African penguins to indicate the primary foraging area in a) 2008, b) 2009 and c) 2010 from Dyer Island, South Africa. Each colour represents an individual foraging trip of a single bird.

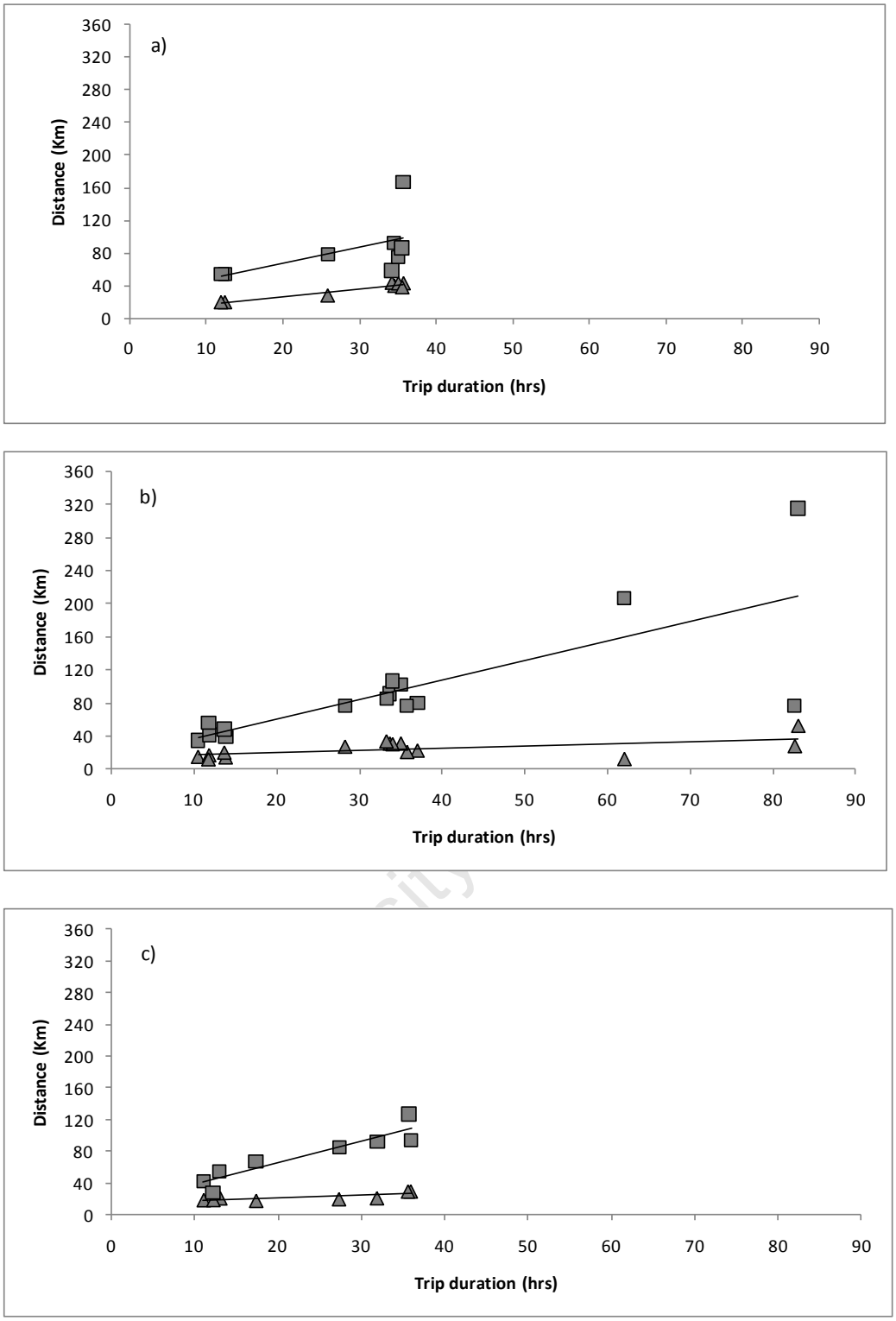

Figure 6: Relationship between trip duration (hrs) and foraging range (km) (maximum distance from the nest) (triangles) and the total distance travelled (squares) for African penguins from Dyer Island, South Africa, in a) 2008 (n = 8 birds); b) 2009 (n=15 birds) and c) 2010 (n=8 birds).

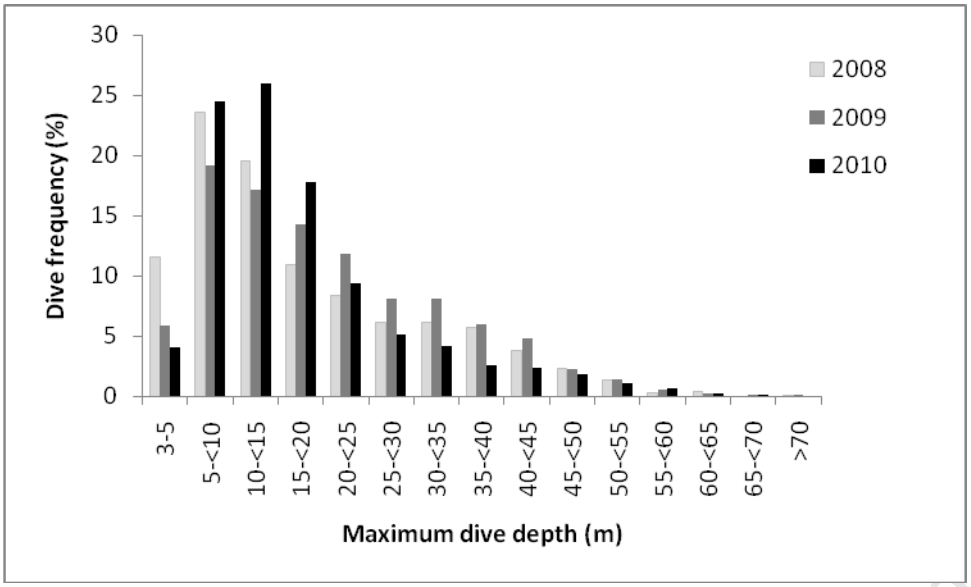

Figure 7: Dive frequency in 5m intervals (first interval comprises dives ≥ 3 – <5 m) for African penguins on Dyer Island, South Africa, in 2008, 2009 and 2010.

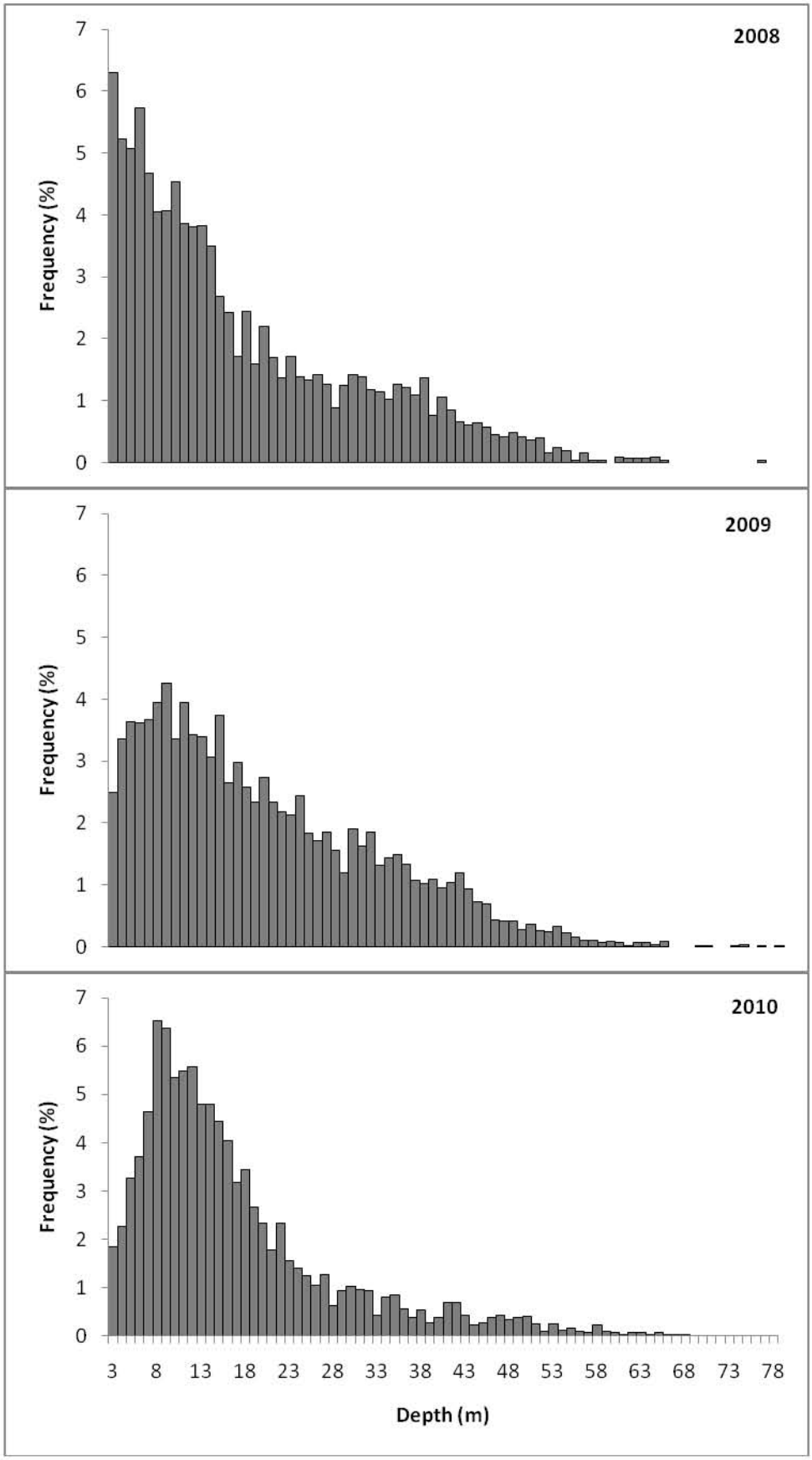

Figure 8: Frequency distribution of dive depths > 3 m by adult African penguins breeding at Dyer Island for 2008 (n=3 313), 2009 (n=4 925) and 2010 (n=3215).

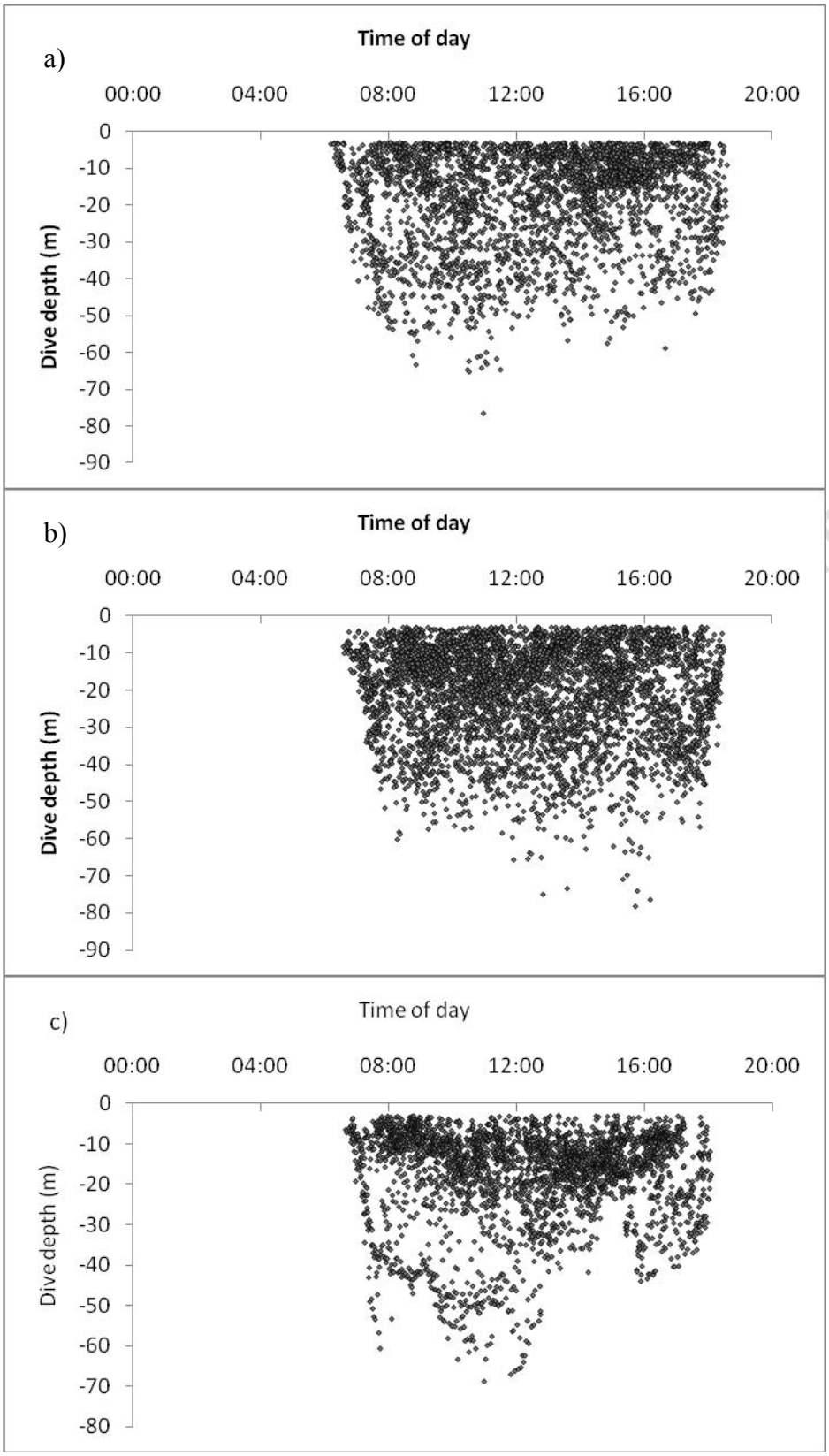

Figure 9: Maximum dive depth (m) in relation to time of day for African penguins at Dyer Island, South Africa, in a) 2008, b) 2009 and c) 2010

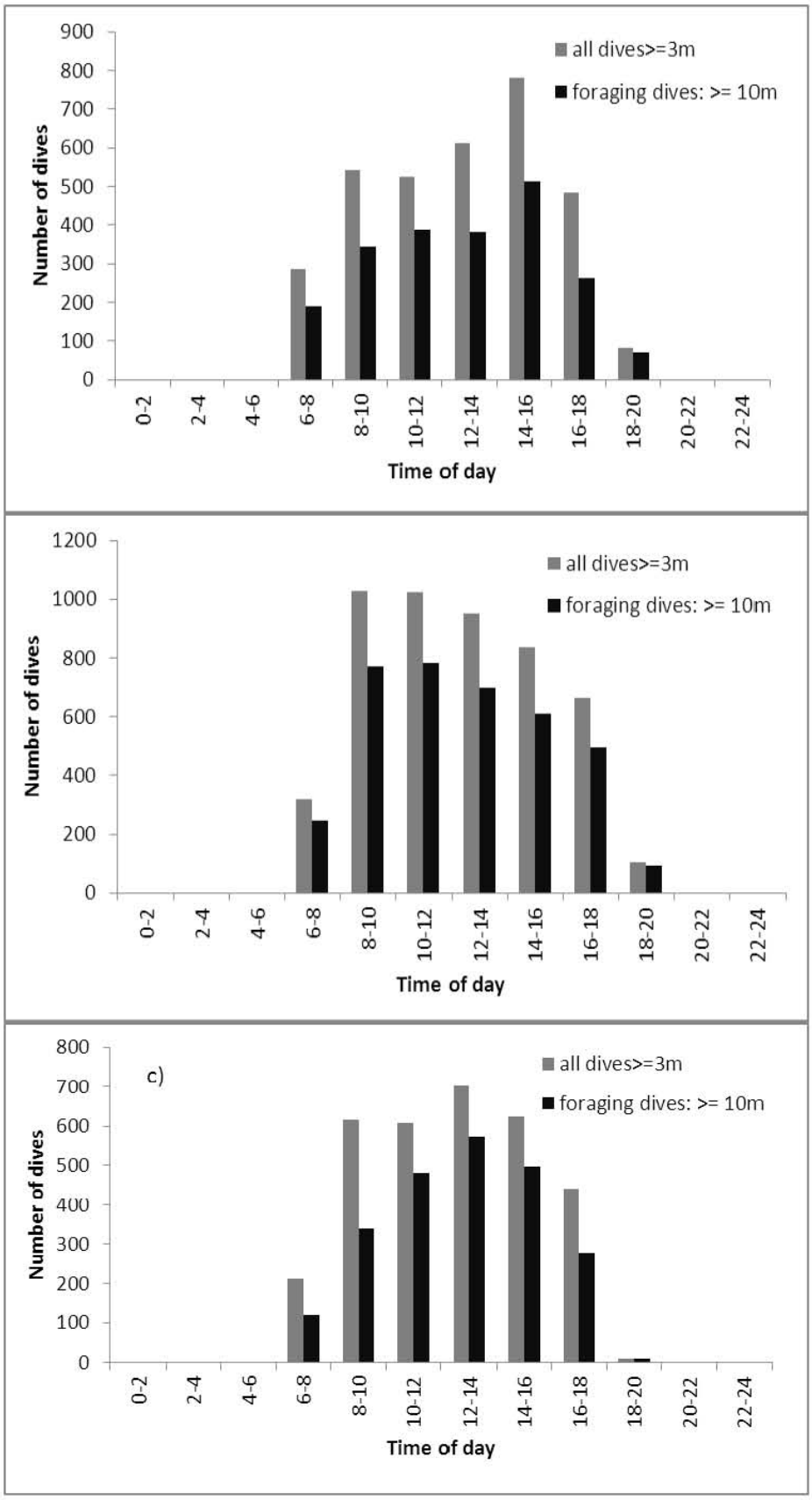

Figure 10: Relationship between number of dives (all dives > 3 m) and foraging dives (dives ≥ 10 m) and time of day for African penguins on Dyer Island, South Africa, in a) 2008 (n = 7 birds), b) 2009 (n= 9 birds) and c) 2010 (n= 7 birds).

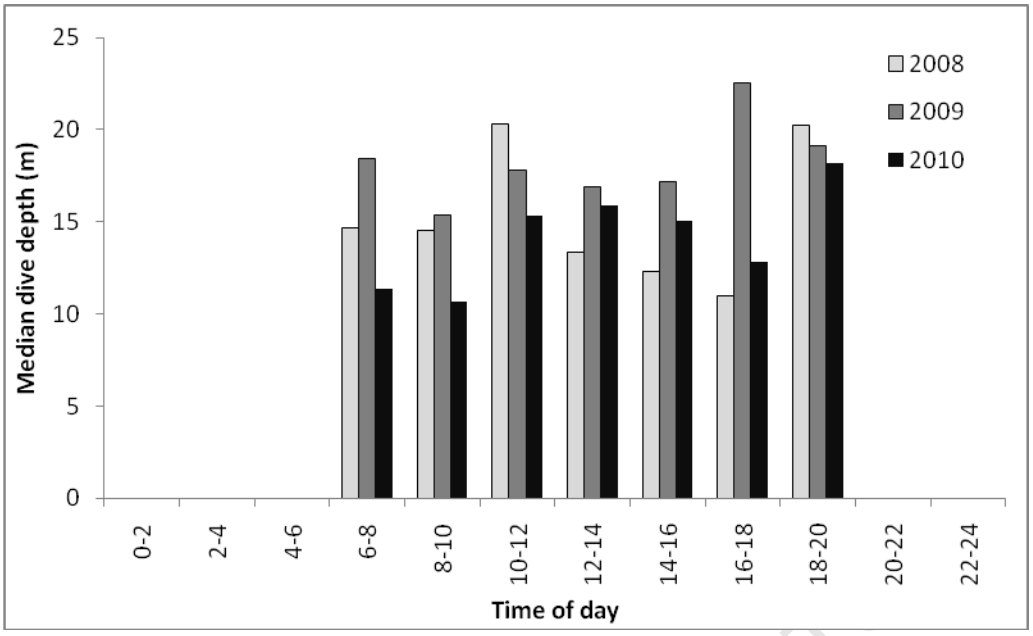

Figure 11: Distribution of number of dives ≥ 3 m of African penguins from Dyer Island, South Africa, in 2008, 2009 and 2010 in relation to the time of day.

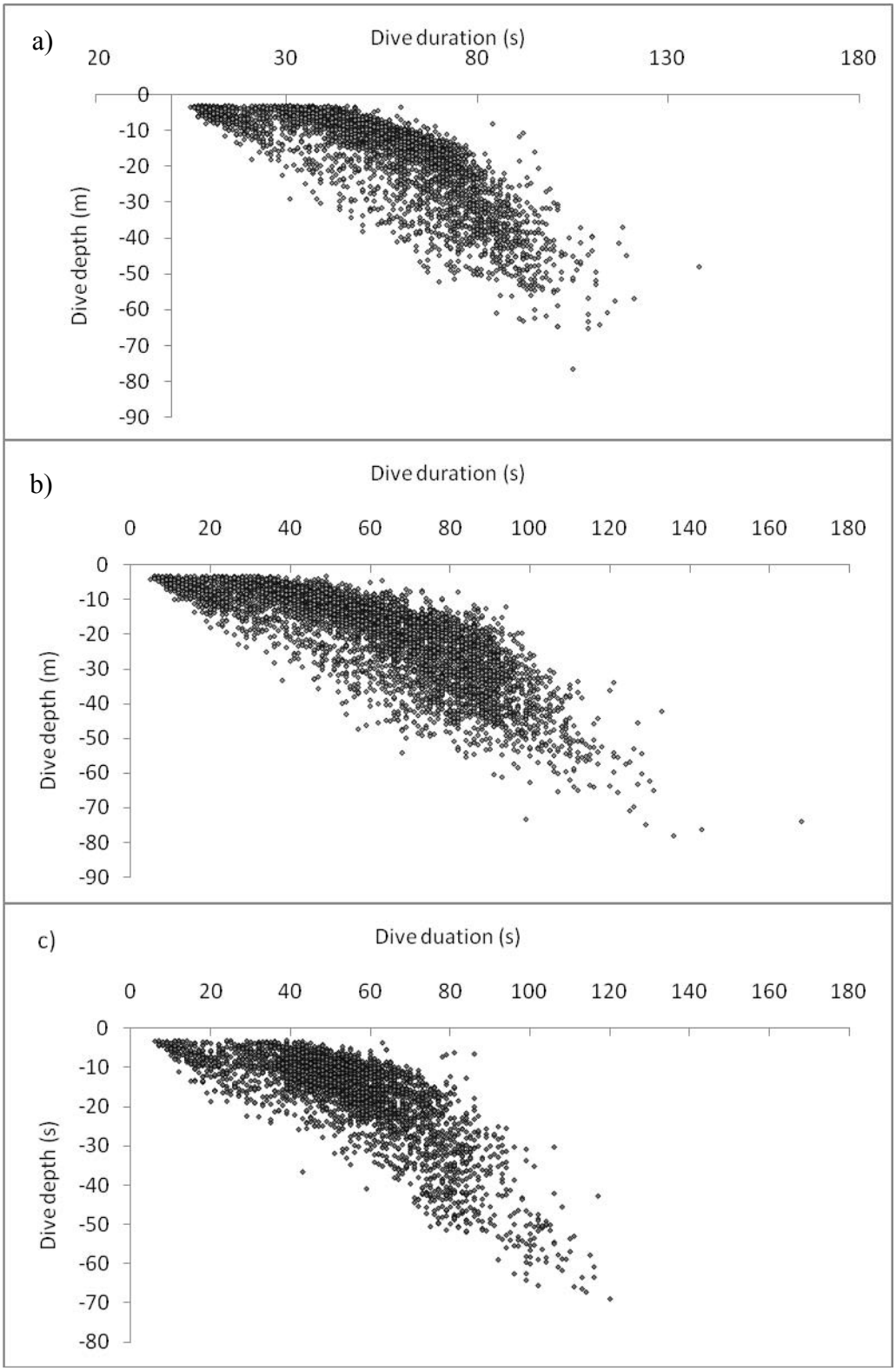

Figure 12: Relationship between dive duration (s) and dive depth (m) for African penguins from Dyer Island, South Africa, in a) 2008 (n = 3313 dives), b) 2009 (n = 4295 dives) and c) 2010 (n= 3215 dives).

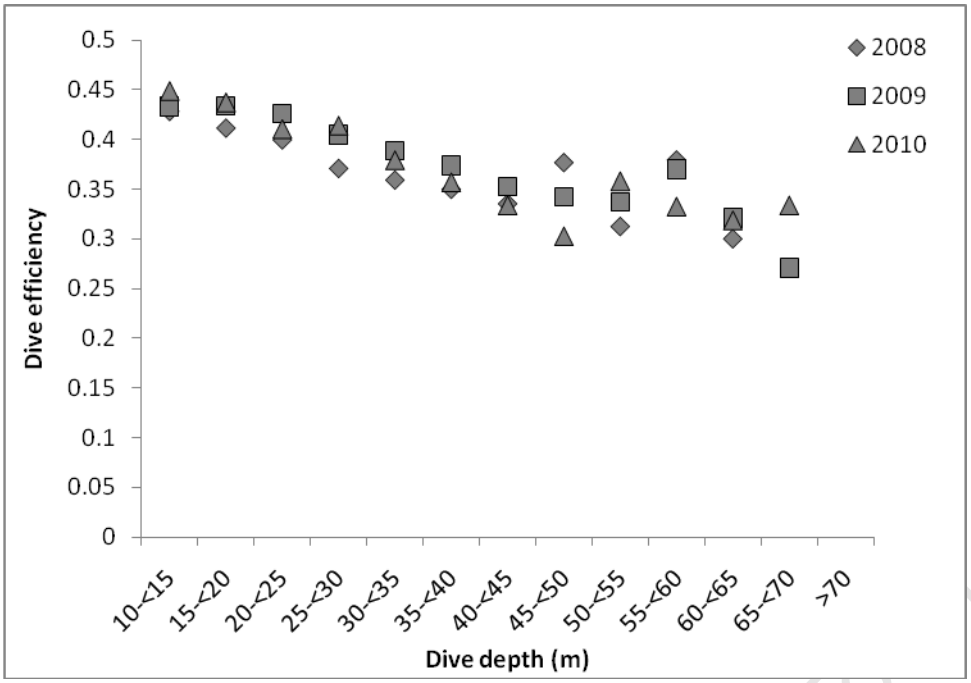

Figure 13: Relationship between dive depth (m) and dive efficiency for foraging dives of African penguins from Dyer Island, South Africa, in 2008, 2009 and 2010.

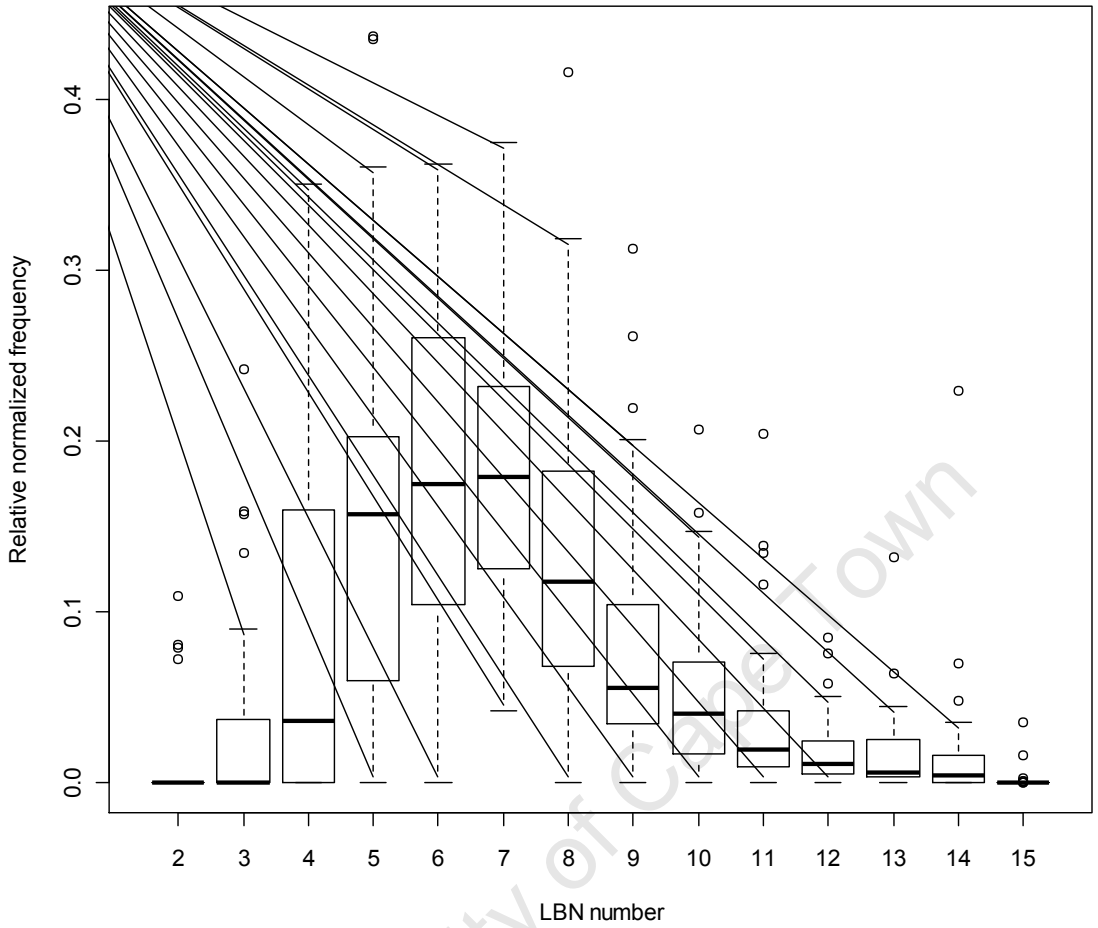

Figure 14:. Box and whisker plot of distance-ratio scale (DRS) values according to log-binning classes for all African penguin *Spheniscus demersus* tracks combined. The range of DRS values (m) that each log-binning class covers is twice the preceding one: 2 (3–4); 3 (5–8); 4 (9–16); 5 (17–32); 6 (33–64); 7 (65–128); 8 (129–256); 9 (257–512); 10 (513–1 024); 11 (1 025–2 048); 12 (2 049–4 096); 13 (4 097–8 192); 14 (8 193–16 384); 15 (16 385–32 768).

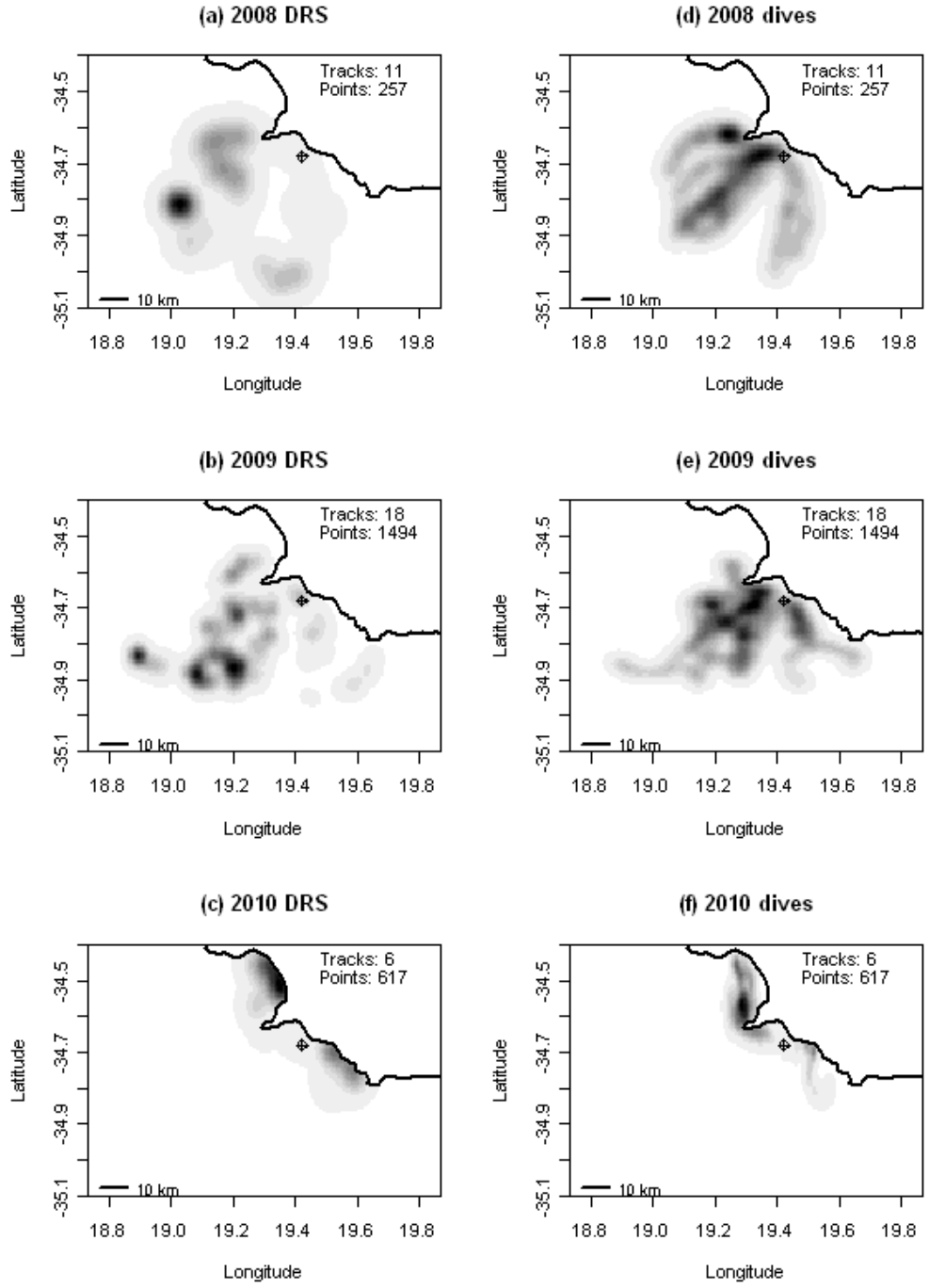

Figure 15: Kernel density estimation of fine-scale DRS and dive positions of African penguin foraging off Dyer Island during three years. Densities were estimated on a 0.00625° × 0.00625° grid (*c.* 0.69×0.59 km); data included both complete and incomplete tracks. Grey intensity indicates increasing densities per unit area. The location of Dyer Island is indicated by the diamond-shaped symbol. Overlap measured with Morisita's Index as modified by Horn (Ricklefs and Lau 1980) between fine-scale DRS and dives densities were 38.0, 52.0, and 31.8% for 2008, 2009 and 2010 respectively.

Appendix 1: Sea going rhythm of African penguins on Dyer Island in 2010 for the period 19 May–28 May. U refers to unmarked birds and P refers to 'pink' which were the marked birds.

			19-May-10		20-May-10		22-May-10	23-May-10		24-May-10			25-May-10			26-May-10		27-May-10			28-May-10	
Nest No.	Nest ID	Ad ID	15:15	19:00	08:30	18:00	16:00	14:30	19:00	08:00	12:00	18:00	08:00	14:00	18:00	08:00	16:00	09:35	14:22	17:30	10:10	18:00
1	Q5	F1957 (Pink)	P	P	P		P											P	P	P	P	
		F1902 (U)				U			U	U	U	U	U	U	U	U	U					U
2	Cem28*	F1891 (Pink)	P			P	P		P	P	P	P				P	P	P	P			
		F1951 (U)		U	U								U	U	U					U	U	U
3	Cem2*	F1929 (Pink)	P						P				P	P	P			P	P	P	-	P
		F1802 (U)		U	U	U	U			U	U	U				U	U				-	
4	Cem34	F1992 (Pink)	P						P							P	P				P	P
				U	U	U	U			U	U	U	U	U	U			U	U	U		U
5	Cem4	F1974 (Pink)	P	P					P				P	P	P					P	P	P
					U	U	U			U	U	U				U	U	U	U			U
6	Cem21*	F1837 (Pink)	P	P									P	P	P			P	P	P		
		F1803 (U)		U	U	U	U		U	U	U	U				U	U				U	U
7	Cem22	F1888 (Pink)					P		P	P	P	P				P	P	P	P	P		
		F1840/9 (U)							U				U	U	U						U	U
8	OldB8*	F1823 (Pink)	P	P			P				?	?				P	P				P	
				U	U	U			U	P?				?	U			U	U	U		
9	OldB10	F1844 (Pink)	P	P			P		P	P	P	P				P	P				P	P
		A12042 (U)			U	U			U				U	U	U			U	U	U		
10	Cem48*	F1843 (Pink)	P	P	P		P		P	P	P	P						P	P	P	-	
		F1864 (U)				U			U				U	U	U	U	U				-	U
11	LU1*	F1858 (Pink)	P	P					P				P	P	P			P	P	P	P	P
		F1863		U	U	U	U		U	U	U	U				U	U					U
12	LU4	F1971 (Pink)	P	P			P		P	P	P	P				P	P				P	
				U	U	U			U				U	U	U			U	U	U		U
13	H9	F1917 (Pink)	P	P	P	P	P		P	P	P	P	P	P	P			P	P			
		F1982 (U)				U			U						U	U	U			U	U	U
14	H13*	F1964 (Pink)	P	P			P					P	P	P		P	P	P	P	P		P
		F1963 (U)			U	U			U	U	U				U						U	U
15	H14	F1993 (Pink)	P	P		P						P	P	P			P	P	P	P	P	P
				U	U	U	U		U	U	U				U	U						U
16	R 3	Pink	P	P	P	P	P												P			
				U					U	U	U	U	U	U	U	U	U	U		U	U	U
17	Y1	F1911 (Pink)	P			P						P	P	P	P			P	P	P		
				U	U		U		U	U	U					U	U			U	U	U
18	CP8*	Pink	P	P	P		P		U	P	?	?	?	P	P			P		P		
						U										U	U				U	U
19	CP14*	Pink	P	P	P			p back at 1	P	P	P					P	P			P	P	P
						U	U					U	U	U	U			U	U	U		U

* Logger Birds

Appendix 2: GPS-TD logger settings and deployment summaries for equipped birds on Dyer Island, South Africa in 2008, 2009 and 2010.

BIRD ID	Complete Track	GPS Sampling Interval	Temperature & Pressure Sampling Interval	Required Satellites	Search Limit	Max Allowable Search time (min)	Off time (min)
2008							
GPS182_24July08_CP1	Y	01min/00sec	00min/01sec	3	No		
GPS182_26July08_GPS2	Y	01min/00sec	00min/01sec	3	No		
GPS180_26July08_E17	Y	01min/00sec	00min/01sec	3	No		
GPS182_24July08_CP6	Y	01min/00sec	00min/01sec	3	No		
GPS182_28July08_oldA10	2h GPS data missing on way back	30min/00sec	00min/01sec	3	No		
GPS182_26Aug08_CP2	Y	03min/00sec	00min/01sec	3	Yes	5	15
GPS182_28Aug08_E11	N (GPS but no dive data)	03min/00sec	00min/01sec	3	Yes	5	15
GPS180_26Aug08_F5	Y	03min/00sec	00min/01sec	3	Yes	5	15
GPS180_23July08_CP4	Incomplete (trip longer than battery)	01min/00sec	00min/01sec	3	No		
GPS181_24July08_Toilet	Incomplete (trip longer than battery)	01min/00sec	00min/01sec	3	No		
GPS180_28July08_oldA2	Incomplete (trip longer than battery)	30min/00sec	00min/01sec	3	No		
GPS181_27Aug08_oldA7	N (bird didn't leave)	03min/00sec	00min/01sec	3	Yes	5	15
GPS183_24July08_CO4	N(download problem - no data)	01min/00sec	00min/01sec	3	No		
GPS183_25July08_CO4	N(download problem - no data)	01min/00sec	00min/01sec	3	No		
GPS182_25July08_CP20	N(download problem - no data)	01min/00sec	00min/01sec	3	No		
GPS181_26July08_E5	N (bird didn't leave)	01min/00sec	00min/01sec	3	No		
2009							
GPS182_27May09_Q8	N (no sensor data, download failed)	01min/00sec	00min/01sec	3	No		
GPS183_27May09_Wall	N (no sensor data, download failed)	01min/00sec	00min/01sec	3	No		
GPS180_27May09_CP7	Y	01min/00sec	00min/01sec	3	No		
GPS181_27May09_CP33	Incomplete (trip longer than battery)	01min/00sec	00min/01sec	3	No		
GPS183_28May09_CEM46	N (no sensor data, download failed)	01min/00sec	00min/01sec	3	No		
GPS180_29May09_CP25	N (bird did not leave)	01min/00sec	00min/01sec	3	No		
GPS182_30May09_CEM48	Y	01min/00sec	00min/01sec	3	No		
GPS183_30May09_CEM28	Y	01min/00sec	00min/01sec	3	No		
GPS180_30May09_CEM3	N (bird did not leave)						
GPS180_1June09_CEM17	N (bird did not leave)						
GPS181_1June09_E1	N (no sensor data, download failed)	01min/00sec	00min/01sec	3	No		
GPS183_1June09_OldB1	N (trip longer than battery + no sensor data, download pb)	01min/00sec	00min/01sec	3	No		
GPS182_21July09_E10	Y	01min/00sec	00min/01sec	3	No		
GPS183_22July09_CP21	N (no sensor data, download failed)	01min/00sec	00min/01sec	3	Yes	5	15
GPS181_22July09_E13	N (bird did not leave)						
GPS244_22July09_CP15	Y	01min/00sec	00min/01sec	4	Yes	5	30
GPS182_22July09_E1	N (trip longer than battery +no sensor data, download pb)	01min/00sec	00min/01sec	3	No		
GPS243_23July09_CP4	Y	01min/00sec	00min/01sec	3	Yes	5	30
GPS180_24July09_K4	Y	01min/00sec	00min/01sec	3	Yes	5	15
GPS244_24July09_K20	Y	01min/00sec	00min/01sec	4	Yes	4	15
GPS182_24July09_K37	Y	01min/00sec	00min/01sec	3	Yes	5	30
GPS180_27July09_WallB*	Incomplete (trip longer than battery)	01min/00sec	00min/01sec	3	No		
GPS182_27July09_H13	N (wet)	01min/00sec	00min/01sec	3	No		
2010							
244_22May10_CP8	Y	01min/00sec	00min/01sec	3	Yes	5	15
183_22May10_H13	N (no dive data)	00min/01sec	00min/01sec	3	Yes	5	15
243_22May10_OLDB8	Y	01min/00sec	00min/01sec	3	Yes	5	10
244_24May10_CEM2	Y	01min/00sec	00min/01sec	3	Yes	5	15
243_24May10_CP14	Y	01min/00sec	00min/01sec	3	Yes	5	10
181_26May10_OLDB10	N (bird did not leave)	01min/00sec	00min/01sec	3	Yes	5	10
183_26May10_CEM48	Y	01min/00sec	00min/01sec	4	Yes	5	15
244_26May10_CEM28	Y	01min/00sec	00min/01sec	3	Yes	5	10
243_26May10_LU1	Y	01min/00sec	00min/01sec	3	Yes	5	10
181_26May10_CEM21	N (stopped recording)	01min/00sec	00min/01sec	4	Yes	5	15

For all deployments: Pressure Mode–Upon each surfacing, Activity Interval–No, Pressure Control Enabled: Yes

Appendix 3: Summary of data from GPS-TD equipped African penguins on Dyer Island, South Africa in 2008, 2009 and 2010.

Bird ID	Deployment		Departure		Arrival		Trip	Foraging	Max dist	Loop	Max dive
	Date	Time	Date	Time	Date	Time	Duration (Hrs)	Path length (km)	To nest (km)	factor	Depth (m)
2008											
GPS182_24July08_CP6	23/7/2008	23:00	24/7/2008	6:00	24/7/2008	18:00	12.00	53.62	19.00	2.82	57.60
GPS182_24July08_CP1	24/7/2008	22:15	25/7/2008	5:30	25/7/2008	18:00	12.50	53.95	19.00	2.84	50.96
GPS180_26July08_E17	26/7/2008	20:00	27/7/2008	7:10	28/7/2008	18:50	35.67	166.43	42.43	3.92	76.63
GPS182_26July08_GPS2	26/7/2008	21:00	27/7/2008	14:30	28/7/2008	16:20	25.83	78.71	27.30	2.88	49.50
GPS182_28July08_oldA10	28/7/2008	23:00	29/7/2008	6:30	30/7/2008	17:00	34.50	92.09	39.25	2.35	64.73
GPS180_26Aug08_F5	26/8/2008	20:00	27/8/2008	5:30	28/8/2008	17:00	35.50	86.20	37.46	2.30	65.30
GPS182_26Aug08_CP2	26/8/2008	21:10	27/8/2008	8:20	28/8/2008	18:30	34.17	58.45	43.03	1.36	61.34
GPS182_28Aug08_E11	28/8/2008	20:15	29/8/2008	6:30	> 26/7/2008	17:30	35.00	75.34	42.31	1.78	65.30
GPS180_23July08_CP4	23/7/2008	23:15	24/7/2008	17:15	> 26/7/2008	6:30	> 37.25	U	34.12		53.01
GPS181_24July08_Toilet	24/7/2008	22:30	25/7/2008	6:45	> 30/7/2008	4:20	> 21.58	U	45.58		67.22
2009											
GPS181_27May09_CP33	27/5/2009	20:30	28/5/2009	5:35		U	U	U	17.61	U	47.33
GPS182_27May09_Q8	27/5/2009	21:00	28/5/2009	3:30	29/5/2009	16:30	37.00	80.29	22.17	3.62	*
GPS183_27May09_Wall	27/5/2009	21:30	28/5/2009	4:40	28/5/2009	18:30	13.83	38.53	13.98	2.76	*
GPS180_27May09_CP7	27/5/2009	22:00	28/5/2009	6:35	28/5/2009	20:15	13.67	48.31	19.77	2.44	65.4
GPS183_28May09_CEM46	28/5/2009	21:00	29/5/2009	5:35	30/5/2009	17:20	35.75	76.76	20.49	3.75	*
GPS182_30May09_CEM48	30/5/2009	18:00	31/5/2009	7:25	1/6/2009	17:05	33.67	91.19	30.61	2.98	78.2
GPS183_30May09_CEM28	30/5/2009	18:10	31/5/2009	7:30	31/5/2009	18:00	10.50	34.41	14.63	2.35	55.00
GPS181_1June09_E1	1/6/2009	19:00	2/6/2009	6:45	2/6/2009	18:35	11.83	41.48	16.57	2.50	*
GPS182_21July09_E10	21/7/2009	19:00	22/7/2009	6:30	23/7/2009	17:30	35.00	102.57	30.65	3.35	57.40
GPS183_22July09_CP21	22/7/2009	14:00	22/7/2009	15:00	23/7/2009	19:15	28.25	77.10	26.91	2.86	*
GPS244_22July09_CP15			23/7/2009	6:15	23/7/2009	18:00	11.75	56.25	11.65	4.83	53.75
GPS243_23July09_CP4	23/7/2009	19:15	24/7/2009	6:40	27/7/2009	17:40	83	315.55	52.12	6.05	59.54
GPS180_24July09_K4	24/7/2009	15:00	25/7/2009	6:25	26/7/2009	16:25	34	106.34	29.89	3.56	46.81
GPS244_24July09_K20	24/7/2009	15:30	26/7/2009	3:45	28/7/2009	17:45	62	207.22	11.97	17.32	74.97
GPS182_24July09_K37	24/7/2009	18:00	25/7/2009	6:45	26/7/2009	16:00	33.25	85.69	33.35	2.57	64.01
GPS180_27July09_WallB*	27/7/2009	17:00	28/7/2009	7:25	31/7/2009	18:00	82.58	76.68	27.58	2.78	47.89
* data interpolated											
2010											
GPS243_OldB8	22/5/2010	18:00	23/5/2010	7:20	23/5/2010	18:20	11.00	41.39	18.45	2.243292	53.88
GPS244_CP8	22/5/2010	18:00	23/5/2010	7:00	23/5/2010	20:00	13.00	54.43	20.72	2.626282	27.80
GPS243_CP14	24/5/2010	15:00	25/5/2010	6:50	25/5/2010	19:00	12.17	27.15	18.65	1.455824	41.83
GPS244_CEM2*	24/5/2010	15:00	25/5/2010	0:50	25/5/2010	18:10	17.33	66.94	17.62	3.798445	39.55
GPS244_CEM28	26/5/2010	16:30	27/5/2010	15:30	28/5/2010	18:50	27.33	84.48	19.66	4.298038	60.72
GPS183_CEM48	26/5/2010	17:00	27/5/2010	5:30	28/5/2010	17:30	36.00	93.75	29.42	3.186895	51.86
GPS243_LU1	26/5/2010	17:15	27/5/2010	5:30	28/5/2010	17:10	35.67	126.35	29.29	4.314381	68.89
GPS183_H13	22/5/2010	18:00	23/5/2010	7:05	24/5/2010	15:00	31.92	91.68	20.90	4.385799	*
GPS181_CEM21-incpl	23/5/2010	18:00	24/5/2010	7:00	*	*	*	*	*	*	*

Appendix 4: Dive data summary for GPS–TD equipped African penguins from Dyer Island in 2008

	Overall Dives (>3m)												Foraging Dives (> 10m)										
	CP1	CP6	CP2		GPS2		OldA10		E17		F5		CP1	CP6	CP2		GPS2		OldA10		E17		F5
			Day 1	Day 2	Day 1	Day 2	Day 1	Day 2	Day 1	Day 2	Day 1	Day 2			Day 1	Day 2	Day 1	Day 2	Day 1	Day 2	Day 1	Day 2	Day 1
6-7	4	0	0	27	0	1	0	5	0	1	0	29	0	0	0	14	0	1	0	2	0	0	0
7-8	39	8	0	18	0	35	0	38	3	35	15	27	12	0	0	12	0	32	0	38	0	35	4
8-9	19	40	2	21	0	12	7	31	44	20	8	29	14	33	0	4	0	11	0	30	3	17	7
9-10	13	27	33	21	0	26	29	28	51	31	12	39	7	24	0	15	0	23	29	27	36	25	4
10-11	31	26	31	26	0	12	39	30	53	33	0	32	15	22	13	24	0	8	38	25	43	26	0
11-12	2	39	7	11	0	20	15	34	28	36	7	12	2	30	5	1	0	15	13	22	22	22	7
12-13	2	34	27	37	0	29	19	37	23	39	17	23	2	12	0	24	0	18	18	36	19	31	13
13-14	7	19	48	41	0	34	29	28	41	38	13	27	6	12	11	29	0	19	24	20	20	34	6
14-15	30	37	45	43	13	39	35	24	16	48	6	42	22	20	18	38	3	34	35	4	4	41	2
15-16	10	31	36	58	40	40	37	1	29	49	14	58	6	21	18	34	25	8	28	0	26	47	7
16-17	3	10	19	14	45	10	25	2	38	60	16	18	3	2	5	5	43	0	23	0	25	22	12
17-18	3	10	35	0	31	0	44	2	35	55	10	0	0	0	31	0	23	0	33	0	21	1	6
18-19	0	0	22	0	17	0	13	0	16	4	11	0	0	0	16	0	17	0	12	0	15	0	9
19-20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
No. Dives	163	281	305	317	146	258	292	260	377	449	129	336	89	176	117	200	111	169	253	204	234	301	77
Start time	6:24	7:32	8:51	6:11	14:44	6:58	8:19	6:47	7:41	6:51	7:33	6:16	7:18	8:01	10:26	6:34	14:49	6:58	9:02	6:51	8:48	7:00	8:48
End Time	17:55	17:36	18:36	16:59	18:22	16:13	18:21	17:24	18:22	18:30	18:33	16:15	16:15	16:18	18:35	16:59	18:22	15:47	18:21	14:58	18:22	17:21	18:22

Appendix 5: Dive data summary for GPS–TD equipped African penguins from Dyer Island in 2009

	Overall Dives > 3m																							
	CP7	CEM28	CP15		K4			E10			CEM48			CP4					K20				K37	
				Total	Day 1	Day 2	Total	Day 1	Day 2	Total	Day 1	Day 2	Total	Day 1	Day 2	Day 3	Day 4	Total	Day 1	Day 2	Day 3	Total	Day 1	Day 2
6-7	0	0	0	7	0	7	0	0	0	5	0	5	0	0	0	0	0	0	0	0	0	18	0	18
7-8	26	0	0	42	3	39	37	0	37	33	0	33	88	0	28	30	30	28	2	0	26	34	0	34
8-9	48	22	31	64	20	44	46	24	22	29	0	29	86	0	39	18	29	91	33	23	35	66	35	31
9-10	53	33	23	74	40	34	67	33	34	54	23	31	80	0	24	22	34	104	30	38	36	57	24	33
10-11	31	21	28	81	39	42	90	50	40	56	20	36	98	17	30	17	34	86	15	30	41	45	17	28
11-12	21	18	21	77	34	43	92	32	60	75	30	45	92	32	26	18	16	44	17	27	0	50	10	40
12-13	26	21	27	84	26	58	74	20	54	60	25	35	63	37	1	23	2	41	20	21	0	76	17	59
13-14	23	33	19	58	20	38	77	26	51	66	31	35	91	26	13	26	26	39	15	24	0	72	16	56
14-15	32	30	24	32	32	0	85	34	51	65	21	44	64	29	0	4	31	40	25	15	0	77	34	43
15-16	18	38	23	32	32	0	53	23	30	59	16	43	72	33	12	12	15	63	33	30	0	30	30	
16-17	0	53	0	30	30	0	29	28	1	36	22	14	90	33	29	28	0	76	48	28	0	28	28	
17-18	2	15	0	35	35	0	30	30	0	25	25	0	102	36	42	24	0	79	46	33	0	32	32	
18-19	0	0	0	18	18	0	11	11	0	0	0	0	49	16	23	10	0	11	4	7	0	15	15	
No. Dives	280	284	196	634	329	305	691	311	380	563	213	350	975	259	267	232	217	702	288	276	138	600	258	342
Start time	7:29	8:27	8:07		7:58	6:44		8:32	7:07		9:16	6:41		10:23	7:14	7:02	7:04		7:54	8:29	7:09		8:18	6:34
End Time	17:12	17:40	15:47		18:22	13:32		18:15	16:16		17:57	16:35		18:24	18:29	18:20	15:23		18:05	18:15	10:55		18:24	14:41

Appendix 5 cont: Dive data summary for GPS–TD equipped African penguins from Dyer Island in 2009

	Foraging Dives > 10 m																							
	CP7	CEM28	CP15		K4			E10			CEM48			CP4				K20				K37		
				Total	Day 1	Day 2	Total	Day 1	Day 2	Total	Day 1	Day 2	Total	Day 1	Day 2	Day 3	Day 4	Total	Day 1	Day 2	Day 3	Total	Day 1	Day 2
6-7	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	9
7-8	8	0	0	37	0	37	28	0	28	29	0	29	78	0	23	26	29	26	0	0	26	30	0	30
8-9	19	11	22	46	3	43	32	11	21	28	0	28	80	0	38	17	25	52	19	1	32	42	15	27
9-10	24	30	21	64	34	30	50	26	24	51	20	31	74	0	23	20	31	73	22	19	32	51	20	31
10-11	22	16	25	67	34	33	28	11	17	49	15	34	80	3	29	14	34	66	14	26	26	35	13	22
11-12	21	17	14	65	30	35	59	30	29	70	30	40	70	21	24	13	12	42	15	27	0	36	8	28
12-13	18	20	18	71	25	46	47	19	28	57	25	32	57	36	0	21	0	35	18	17	0	56	14	42
13-14	23	25	14	25	19	6	29	20	9	62	30	32	66	23	6	18	19	35	12	23	0	40	8	32
14-15	26	27	9	25	25	0	55	26	29	59	19	40	57	26	0	2	29	38	25	13	0	39	16	23
15-16	18	30	2	21	21	0	32	21	11	53	16	37	55	30	5	6	14	44	25	19	0	22	22	0
16-17	0	13	0	23	23	0	23	23	0	26	21	5	76	31	26	19	0	48	23	25	0	20	20	0
17-18	2	6	0	30	30	0	29	29	0	25	25	0	82	32	31	19	0	64	38	26	0	27	27	0
18-19	0	0	0	16	16	0	9	9	0	0	0	0	43	16	17	10	0	10	3	7	0	13	13	0
No. Dives	181	195	125	493	260	233	421	225	196	509	201	308	818	218	222	185	193	533	214	203	116	420	176	244
Start time	7:32	8:31	8:13		8:36	6:47		8:41	7:10		9:17	7:04		18:24	7:14	7:17	7:04		8:15	8:36	7:09		8:25	6:35
End Time	17:12	17:36	15:14		18:22	13:14		18:15	15:43		17:57	16:25		10:31	18:24	18:20	15:21		18:05	18:15	10:55		18:24	14:40

Appendix 6: Dive data summary for GPS–TD equipped African penguins from Dyer Island in 2010

	Overall Dives >3m													Foraging Dives > 10m											
	OldB8	CP8	CP14	CEM2	LU1			CEM28			CEM48			OldB8	CP8	CP14	CEM2	LU1			CEM28			CEM48		
	Day 1	Day 1	Day 1	Day 1	Day 1	Day 2	Day 3	Day 1	Day 2	Day 3	Day 1	Day 2	Day 3	Day 1	Day 1	Day 1	Day 1	Day 1	Day 2	Day 3	Day 1	Day 2	Day 3	Day 1	Day 2	Day 3
6-7	0	0	0	7	0	0	0	7	0	7	13	0	13	0	0	0	0	0	0	0	4	0	4	1	0	1
7-8	7	17	0	42	45	16	29	34	0	34	39	1	38	3	1	0	21	24	0	24	32	0	32	32	0	32
8-9	40	50	31	40	66	31	35	30	0	30	67	39	28	20	13	1	25	35	2	33	19	0	19	30	2	28
9-10	46	31	32	31	63	30	33	26	0	26	65	38	27	34	11	18	19	56	24	32	20	0	20	40	13	27
10-11	42	50	47	28	63	31	32	41	0	41	59	34	25	26	43	45	26	41	16	25	37	0	37	55	30	25
11-12	47	43	21	13	66	37	29	21	0	21	69	38	31	38	37	17	13	38	12	26	20	0	20	44	16	28
12-13	34	58	41	25	66	35	31	44	0	44	73	36	37	28	46	37	22	49	19	30	31	0	31	50	17	33
13-14	52	49	43	34	68	35	33	36	0	36	78	33	45	44	42	39	31	51	26	25	32	0	32	71	27	44
14-15	54	59	42	46	61	43	18	43	0	43	42	40	2	45	52	40	35	52	35	17	41	0	41	36	34	2
15-16	34	56	33	34	40	37	3	44	0	44	37	37		8	49	12	7	39	36	3	43	0	43	37	37	
16-17	44	41	42	44	35	35		56	26	30	32	32		2	29	16	11	29	29		52	25	27	30	30	
17-18			15		41	41		63	43	20	28	28						37	37		44	32	12	28	28	
18-19					5	5		4	4		0							5	5		4	4		0		
No. Dives	400	454	347	344	619	376	243	449	73	376	602	356	246	248	323	225	210	456	241	215	379	61	318	454	234	220
Start time	7:48	7:40	8:06	6:39		7:36	7:01		16:18	6:49		7:59	6:47	7:49	7:56	8:31	7:21		8;08	7:06		16:18	6:53		8:28	6:57
End Time	16:47	16:39	17:14	16:50		18:06	15:06		18:04	17:57		17:52	14:30	16:15	16:36	16:53	16:42		18:06	15:06		18:04	17:54		17:52	14:30

CHAPTER 6

SOUTH AFRICAN NATIONAL BIODIVERSITY LEGISLATION: CONTEXT FOR THE AFRICAN PENGUIN

Photo: Dyer Island Cruises

SOUTH AFRICAN NATIONAL BIODIVERSITY LEGISLATION: CONTEXT FOR THE AFRICAN PENGUIN

ABSTRACT

The South African biodiversity legislative context for the conservation and protection of the African penguin *Spheniscus demersus* is considered. The principles of the National Environmental Management Act (No. 107 of 1998) are highlighted since it is from this Act that subsequent legislation pertaining to environmental protection, protected area management and biodiversity conservation are drawn. The National Environmental Management: Protected Areas Act (No. 57 of 2003) provides the framework for the management of protected areas. Not all African penguin breeding colonies are protected under this Act and it is recommended that this be addressed. The National Environmental Management: Biodiversity Act (No. 10 of 2004) provides the framework for the management of protected species. Under this Act, the Threatened or Protected Species Regulations have been gazetted, where the African penguin is listed. The implication of this for the African penguin is discussed. The Biodiversity Act makes provision for the compilation of a Biodiversity Management Plan for Species. This process was initiated in March 2010. The manner in which other stakeholders such as scientists and non-governmental can be involved in this plan is highlighted. The Biodiversity Management Plan is considered an appropriate tool for the conservation of the species, and the framework within which the best available science pertaining to this species can be incorporated into policy.

KEYWORDS

African penguin, biodiversity, Biodiversity Management Plan for Species, legislation, National Environmental Management Act, South Africa

INTRODUCTION

The conservation status of the African penguin *Spheniscus demersus* was reclassified from 'Vulnerable' to 'Endangered' on the IUCN Red List in June 2010 (BirdLife International 2010). The justification for this revised status was a rapid population decline, probably as a result of commercial fisheries and shifts in prey populations, that this trend showed no sign of reversing, and that immediate action was required to prevent further declines (BirdLife International 2010). Crawford *et al*. (2011) confirmed

that the 2010 census of the African penguin yielded the smallest population size since the first survey in 1953, and regular surveys between 1970 and 2010. The ongoing rapid decline observed since 2004 has been attributed to insufficient prey, either through competition with commercial fisheries or through a mismatch between the spatial location of the colonies of African penguins and their prey, a consequence of shifting prey resources (Crawford *et al*. 2011).

While the legal mandate for the conservation of this species in South Africa lies with the South African government, other stakeholders conduct research, and undertake education, awareness and rehabilitation programmes, which promote the conservation and protection of this species. There are however, also potential areas of conflict. African penguins feed primarily on pelagic fish, predominantly anchovy and sardine (Rand 1960, Crawford *et al*. 2011) and a link between the declining African penguin population and available fish resources has been suggested (Pichegru *et al*. 2009, Crawford *et al*. 2011). These fish are however, also targeted by the South African pelagic fishing industry, the fishery with the greatest tonnage landed and second most in terms of economic value (Hutchings *et al*. 2009). The South African fishing industry overall contributes a relatively small amount to the country's GDP, yet is an important source for job creation, especially in the arid coastal regions where alternative employment is often scarce (Hutchings *et al*. 2009).

The South African government has a number of roles: the protection of biodiversity on behalf of its citizens for current and future generations, the sustainable use of natural resources, the creation of jobs and economic stability. The benefits to people of conserving biodiversity are being debated and slowly recognised (Blackmore 2006, Paterson 2006). However, with a growing population, pressure on the use of natural resources will increase as government aims to improve the economic and social wellbeing of its citizens. The question arises as to the role of the State in conserving biodiversity, in light of the legislation in place that provides for biodiversity conservation as well as economic and job security.

In light of the African penguin population decline, and the desire of multiple stakeholders to work towards an action plan that will prevent further declines, the process of drafting a Biodiversity Management Plan for Species (BMP-S), in this instance for the African Penguin, was initiated under the National Environment

Management: Biodiversity Act (No. 10 of 2004) in March 2010. This process was facilitated by the Department of Environmental Affairs: Oceans and Coasts sub-directorate and CapeNature, the Western Cape provincial conservation authority. A requirement of the BMP-S document is a description of the legislative context pertaining to the species in question. This chapter provides that description. It aims to give those working within the legislative structures an understanding of the framework within which they work and the biodiversity conservation mandate they are required to implement and enforce. It provides scientists and academic institutions, non-governmental organisations (NGOs), non-profit organisations (NPOs) a means by which they are able to guide and assist government organisations to achieve biodiversity conservation in South Africa.

Much research is conducted on endangered species, in this case the African penguin, many of the studies culminating in sound recommendations for management. Those recommendations can only be effectively and sustainably implemented within a legal framework, involving the mandated statutory agencies. Scientists therefore need to be familiar with the relevant legislative structures and processes in order that they be able to contribute to the decision making process and ensure that their recommendations are implemented effectively. An understanding of the country's legislative structures also gives these tertiary institutions, NGOs, other stakeholders and the public-at-large a means by which they are able to measure compliance of government in carrying out its responsibility and fulfilling its legal mandate. A sound legislative framework provides a mechanism whereby activities or individuals that negatively impact the welfare of this species can be dealt with. Additionally, a good understanding of this legislative framework and the respective mandates that government, NGOs and research institutions carry, will unify all organisations involved in African penguin conservation because it clarifies the framework/scope/reach within which each organisation operates.

The legislation pertaining to biodiversity and conservation in South Africa can appear uncoordinated, fragmented and complicated (Smith 2005, Blackmore 2006). This chapter aims to provide an overview of the biodiversity conservation legislative framework in place in 2010 within the context of the National Environmental Management Acts. It will focus on how these Acts are relevant to the protection and conservation of the African penguin in order that it can become a resource that can be

used to guide readers in the direction needed in order to aid their decision making, or to whom to address their queries.

Background to Environmental Legislation in South Africa

In spite of being a signatory to a number of international conventions that required a commitment to conserve biodiversity (Appendix 1), South Africa's approach to biodiversity conservation prior to 1994 was unstructured and un-coordinated (Smith 2005). Conservation was largely the responsibility of the provinces, all of which had their own ordinances, delegated from national government, which were not consistent with each other, were poorly coordinated and did not provide for adaptation along with the increasing pressures on the environment and species (Blackmore 2006).

The National Environmental Management Act (No. 107 of 1998) and the subsequent promulgation of the Biodiversity Act (No. 10 of 2004) and the Protected Areas Act (No. 57 of 2003) were significant steps in developing a co-ordinated legal framework for biodiversity conservation (Smith 2005, Blackmore 2006). This discussion aims to highlight these Acts, and the implications that they have for biodiversity conservation, specifically with respect to the African penguin. I start by providing an overview of the contextual framework for South Africa's environmental legislation.

Environmental legislation in South Africa is entrenched in the national Constitution through the Bill of Rights (No. 108 of 1966). The Constitution places a responsibility on all organs of state to protect the environment according to the mandates handed down to them via the Constitution, national and provincial acts and provincial ordinances. Laws at various levels of government are promulgated to give effect to the Constitution. These laws guide individuals, institutions and government in environmental decision making (van der Linde and Feris 2010).

While national level legislation forms the bulk of South African environmental law, numerous provincial and local statutes have been enacted (van der Linde and Feris 2010). These laws are usually limited in operation to a specific provincial administration. Provincial legislation and legislation at local government level provide a unique and complimentary regulatory framework for environmental law in South Africa (van der Linde and Feris 2010). In addition to national laws, South Africa has an obligation to incorporate international conventions to which it is a signatory, within its

legislative framework. These international conventions are enabled through national acts.

The South African biodiversity legislative structure can be broadly broken down into three levels. Firstly at a national level, national Acts are gazetted that provide the framework for which legislation is passed. Regulations are gazetted in terms of these national acts and these provide the means by which the Acts are enacted. Norms and standards are published to guide the achievement of the objectives stated within the acts, and policies set considerations that apply to the national acts. The authority to enact/enforce these acts is set out in the Constitution and stated within the contextual pages of the legislative document.

Provincial mandates entail developing and applying provincial legislation as well as national acts. These mandates are delegated by the National Minister or the President, or the office of the Provincial Premier. Historically (pre-1994), the provinces received their conservation mandates (Conservation Ordinances) from either the President or the Minister of Environmental Affairs. Currently, provincial conservation bills or acts are tabled at the provincial legislature.

NATIONAL LEGISLATION

Constitution of the Republic of South Africa Act, No. 108 of 1996

The South African Constitution is the supreme law of the country and any law or conduct inconsistent with the Constitution is invalid (van der Linde and Feris 2010). The Constitution lays the foundation for environmental legislation in South Africa. It places a constitutional mandate on government to protect the environment through reasonable legislative and other measures that prevent pollution and ecological degradation, promote conservation and secure ecological sustainable development and the use of natural resources while promoting justifiable economic and social development (van der Linde and Feris 2010).

Chapter Two of the Constitution contains the Bill of Rights which provides the framework from which all South Africa's National and Provincial legislation is drafted. Sections 7, 8 and 24 of the Bill of Rights are of relevance to African penguin conservation. Section 7 states that the Bill of Rights is a cornerstone of democracy in

South Africa. It enshrines the rights of all people in South Africa and affirms the democratic values of human dignity, equality and freedom and that the state must respect, protect, promote and fulfil the rights in the Bill of Rights.

Section 8 deals with the application of these rights, and states that the Bill of Rights applies to all law, and binds the legislature, the executive, the judiciary and all organs of state. Finally, Section 24 deals specifically with environmental rights, and states that everyone has the right to an environment that is not harmful to their health or well-being; to have the environment protected for the benefit of present and future generations, and finally, through reasonable legislative and other measures that prevent pollution and ecological degradation; promote conservation and secure ecologically sustainable development and use of natural resources while promoting justifiable economic and social development.

The Constitution also lays the foundation for the principles that provide for the effective administration of South Africa's current environmental regulatory framework, environmental decision making and also integrated environmental management. These deal with principles of co-operative government and intergovernmental relations (Chapter 3), legislative authority at various tiers of government (Chapters 4–7), publication of acts, international agreements (Chapter 14), areas of concurrent national and provincial legislative competence (Schedule 4) and exclusive provincial level competence (Schedule 5).

These principles set the foundation for the conservation of the African penguin. All organs of state are to ensure they effectively carry out their respective mandates for the protection of species (in this case the African penguin) for future generations. This chapter will focus on the Acts that are promulgated under the National Environmental Management Act. Before doing so, it is important, for purposes of context, that three other legislative instruments are briefly discussed.

Marine Living Resources Act, Seal and Seabirds Act and Seal and Seabirds Policy

The Marine Living Resources Act (MLRA) (No 18. of 1998), the Seabirds and Seals Protection Act (No. 46 of 1973) as well as the Policy on the Management of Seals, Seabirds and Shorebirds (Notice 1717 of 2007) are three instruments which are commonly associated with the conservation of seabirds.

The preamble to the MLRA states that the act aims to provide for the conservation of the marine ecosystem, the long-term sustainable utilisation of marine living resources and the orderly access to exploitation, utilisation and protection of certain marine living resources and to provide for the exercise of control over marine living resources in a fair and equitable manner to the benefit of all citizens of South Africa. However, despite providing for the conservation of the marine ecosystem in which the African penguin forms part, the definitions provided in the MLRA indicate that it does not specifically relate to the protection of seabirds and seals, and that this Act is focussed on fishing and fishing related activities and the regulation thereof. The definitions of the MLRA do not state explicitly what constitutes a 'marine living resource.' The only definitions that relate directly to biological organisms is definition: xiii "fish" means 'the marine living resources of the sea and the seashore, including any aquatic plant or animal whether piscine or not, and any mollusc, crustacean, coral, sponge, holothurian or other echinoderm, reptile and marine mammal, and includes their eggs, larvae and all juvenile stages, but does not include seabirds and seals.' While some of the objectives and principles in Section 2 of the MLRA include the need to conserve marine living resources (Section 2a); the need to apply precautionary approaches in respect of the management and development of marine living resources (Section 2b); the need to preserve marine biodiversity (Section 2e) and the need to protect the ecosystem as a whole, including species which are not targeted for exploitation (Section 2f), these principles and objectives do not specifically relate to seabirds since they are not adequately defined in the MLRA definitions. The MLRA thus deals primarily with South African fishery issues, and is not an appropriate tool to address the conservation action required to protect other marine life such as seals and seabirds.

The Seabirds and Seals Protection Act (No. 46 of 1973) aims include: to provide for the control over certain islands and rocks; for the protection, and the control of the capture and killing, of seabirds and seals; and for the disposal of the products of seabirds and seals. There are however gaps in this legislation that is pertinent to the conservation of seabirds and seals and thus it is not considered an adequate biodiversity conservation tool. Robben Island, for example, which is an important seabird breeding colony, is not included on Schedule 1 of islands and rocks specified in this Act. Furthermore, this Act predates the principles of co-operative governance that are set out in the National Environmental Management Acts. Given the number of management authorities

involved in seabird breeding colony management and species protection in South Africa, it is an outdated legislative tool.

The policy on the Management of Seals, Seabirds and Shorebirds was gazetted in 2007. The purpose of the policy was to set out the considerations that will apply to the management of Seals, Seabirds and Shorebirds when the Seabirds and Seals Protection Act (No. 46 of 1973) was to be updated. The objectives of this policy are to facilitate and ensure the management of conservation of seals, seabirds and shorebirds; co-operative management; sustainable, non-consumptive use of seals, seabirds and shorebirds; research and monitoring; management of adverse interactions; and the implementation of international obligations. With respect to the African penguin, the policy aims to reduce mortality through incidental capture by fisheries, losses due to introduced predators, insufficient food, displacement from breeding sites, degradation of breeding habitat, disturbance by humans, destruction of nests, oil pollution, other forms of pollution. The policy also places a strong emphasis on co-ordinated, co-operative management of seals, seabirds and shorebirds at a local and regional scale.

The policy recognises the importance of captive breeding programmes, including for conservation purposes and that the holding of seabirds will only be allowed under permit. The need for management of interactions between threatened or near-threatened seabirds that may negatively influence the conservation status of seabirds is also recognised. It specifies management interventions that may be adopted such as culling, removal or relocation of predators, where sound, relevant scientific data is used as a basis for these decisions. However in the absence of conclusive data, the precautionary approach will be adopted. The policy also recognises the need for research and monitoring, and that research should be undertaken to ensure the sound management and conservation of seals, seabirds and shorebird populations.

Within the Department of Environmental Affairs: Marine and Coastal Management context, a number of forums were in place within the department that enabled science to influence management and policy formulation. These were groups, such as the Pelagic Scientific Working Group, that provided input to the Pelagic Management Working Group which in turn would set fish quotas. Another group, the Ecosystem Approach to Fisheries Scientific Working Group (EAF SWG) also provides input into the fishery management decision making process. The gap in this structure however, is that

biodiversity conservation management organisations, either national (South African National Parks) or provincial conservation authorities do not formally constitute part of these working groups. Decisions made within these forums have direct bearing on biodiversity conservation on seabird breeding colonies for example, and this is a gap that needs to be addressed. However in 2010, the Department of Environmental Affairs: Branch of Marine and Coastal Management (MCM) disbanded into two sections under Department of Environmental Affairs: Branch Oceans and Coasts, and the Department of Agriculture Forestry and Fisheries (DAFF). All legislation pertaining to MCM needs to be formally delegated to the new department, and the working groups officially re-constituted under the new departments. It is recommended that the biodiversity mandated conservation bodies be represented on the re-structured working groups and that the proposed new Act (National Environment Management: Oceans Act) which will draw from the current Seals, Seabirds and Shorebirds policy takes into account the areas of concurrent national and provincial legislative competencies that other national and provincial conservation bodies hold.

National Environmental Management Act (NEMA) No. 107, 1998

In light of the current (2011) situation in South Africa, where the national legislation pertaining to seabirds is in flux, this chapter will focus on the National Environment Management Acts. The National Environment Management Act (NEMA) (No. 107 of 1988) aims to provide for co-operative environmental governance by establishing principles for decision-making on matters affecting the environment, institutions that will promote co-operative governance and procedures for co-ordinating environmental functions exercised by organs of state.

Smith (2005) stated that NEMA represents an attempt to move away from the fragmented and uncoordinated approach to environmental management in the past towards integrated and coordinated environmental management. The preamble to NEMA suggests that this is the intention of the State. It stipulates that the environment is a functional area of concurrent national and provincial legislative competence, and all spheres of government and all organs of state must co-operate with, consult and support one another. Furthermore, the preamble states that in order to achieve this, it is desirable that the law should promote certainty with regard to decision-making by organs of state on matters effecting the environment; the law should establish procedures and institutions to facilitate and promote co-operative government

and intergovernmental relations and that the law should establish procedures and institutions to facilitate and promote public participation in environmental governance. NEMA thus sets the scene to promote co-operation between national and provincial environmental competencies, a framework for which to achieve this, as well as acknowledge the importance of public participation in environmental governance.

There are a number of statutory stakeholders involved in African penguin conservation: several national government departments, provincial government departments and local municipalities, all of which operate according to their respective mandates and jurisdiction according to their role in African penguin protection and management. Tertiary academic institutions are involved in research; rehabilitation facilities provide an essential service to an endangered species. Zoos and aquaria also have a conservation and captive breeding role in addition to exhibits. All require permits to engage their activity. Which permits and where they get them from is often cause for confusion, especially in some cases where multiple government departments have jurisdiction over an area and/or species.

The principles of the NEMA outline the intent of the State to facilitate effective environmental protection and governance, which if applied correctly, facilitate the involvement of all stakeholders and provide the tools to effectively protect the African penguin. It is important for all stakeholders to understand the principles under which this Act is drafted, since it 'sets the scene' in a sense for two additional Acts which will be discussed later on this chapter which are of particular relevance to African penguin conservation. Of importance to note in the principles below is the State's acknowledgement of its role to protect the environment and to interpret and implement other laws pertaining to protection of the environment. This speaks directly to facilitating the interaction of government agencies such as those tasked to protect and manage the environment under this and other NEM Acts, as well as to departments such as DAFF, tasked to set quotas for pelagic fish, of which species such as the African penguin depend.

The principles set out in the NEMA are set out in Chapter 1 of the Act, and apply throughout the Republic and to the actions of all organs of state that may significantly affect the environment. These principles: acknowledge the State's responsibility to respect, protect, promote and fulfil the social and economic rights in Chapter 2 of the

Constitution (Section 2(1a)); serve as the general framework within which environmental management and implementation plans must be formulated (Section 2(1b)); serve as guidelines by reference to which organs of state must exercise any function when taking any decisions in terms of this Act or statutory provisions concerning the protection of the environment (Section 2(1c)) and guide the interpretation, administration and implementation of this Act, and any other law concerned with the protection and management of the environment. The principles go on to state that environmental management must place people and their needs at the forefront of its concern, and serve their physical, psychological, developmental, cultural and social interests equitably (Section 2(2)).

Section 2(4) of the NEMA principles deals with sustainable development. The IUCN definition for sustainable development includes using natural resources in a way that avoids irreversible damage to ecosystem structure and function, the loss of irreplaceable features or a reduction in ecosystem resilience. The definition also states that environmental interests must be considered alongside social and economic interests, so as to prevent the irreplaceable loss of natural features, function or processes and to ensure a long-term and dependable flow of benefits from the exploitation of renewable resources. Furthermore, it states that delivering such sustainable development will involve significant measures to recover ecosystem structure and function, where the flow of benefits is already reduced or impaired, or where ecosystem resilience is at risk (IUCN 2011). This definition of sustainable development includes sustainable fisheries, since fish are considered a natural resource as defined by the IUCN (IUCN 2011). This shows how the aims and objectives of the MLRA and NEMA are complimentary, and Section 4 of NEMA should then be read with the MLRA principles.

Section 2(4) of NEMA acknowledges that environmental management must be integrated, that all elements of the environment are linked and interrelated and that environmental management must take into account the effects of decisions on all aspects of the environment and all people in the environment by pursuing the selection of the best practise environmental option (Section 2 (4b)). Of particular importance to this discussion is that participation of all interested and affected parties in environmental governance must be promoted (Section 2 (4f)). Decisions must take into account the interests, needs and values of all interested and affected parties (Section 2 (4g)), decisions to be taken in an open and transparent manner (Section 2 (4k)). There

must be intergovernmental co-ordination and harmonisation of policies, legislation and actions relating to the environment (Section 2 (4l)). Global and international responsibilities relating to the environment must be discharged in the national interest (Section 2 (4n)). The environment is held in public trust for the people and the environment must be protected as the people's common heritage (Section 2 (4o)). The cost of remedying pollution and environmental degradation must be paid for by those responsible (Section 2 (4p)) and finally that sensitive, vulnerable, highly dynamic or stressed ecosystems, such as coastal shores, estuaries, wetlands and similar systems require specific attention in management and planning processes (Section 2 (4r)).

These principles ensure that environmental management planning incorporate activities that are adjacent to breeding colonies, for example Section 2 (4b,f,g,h). This section on sustainable development indicates for example, that it should be obligate on the state to avoid oiling and through cooperative governance, for the marine pollution unit of the Department of Environmental Affairs to effect this with relevant provincial and municipal bodies. Wolfaardt *et al*. (2008, 2009) showed that the measure of de-oiling African penguins impacted through oil spills is an effective conservation measure. There is however a physiological cost to the penguin of having been oiled (Wolfaardt *et al*. 2008, 2009), and so the state needs to ensure that these events are avoided, and when they do occur, that the reaction response time is immediate.

The National Environment Management Act thus sets the scene for the environmental management in South Africa, and is the basis from which additional environmental legislation is drafted. For the purposes of legislation pertaining to providing protection to the African penguin, the discussion will now focus on two additional National Acts that have been drafted under NEMA.

National Environmental Management: Protected Areas Act (NEM: PAA) No. 57 of 2003

The objectives of the National Environmental Management Act: Protected Areas Act (NEM: PAA) (No. 57 of 2008) are stated in Chapter 1 of Section 2, and include the provision, within the framework of national legislation, including the National Environmental Management Act, for the declaration and management of protected areas (2a); for co-operative governance in the declaration and management of protected areas (2b); to effect a national system of protected areas in South Africa as part of a strategy to manage and conserve it's biodiversity (2c); to provide for a representative

network of protected areas on state land, private land and communal land (2d); to promote sustainable utilisation of protected areas for the benefit of people in a manner that would preserve the ecological character of those areas (2e); and to promote the participation of local communities in the management of protected areas where appropriate (2f).

In Section 3, NEM: PAA re-affirms the State's trusteeship of protected areas in the Republic, in fulfilling the rights contained in Section 24 of the constitution, and NEM: PAA is said to be binding on all organs of state (Section 4(2)). NEM: PAA expressly states that it needs to be interpreted and applied in accordance with the national environmental management principles (Section 5 (1a)), and be read with the applicable provisions of NEMA (Section 5 (1b)). Additionally NEM: PAA must, in relation to any protected area, be read, interpreted and applied in conjunction with the Biodiversity Act (Section 6). NEM: PAA does not affect the implementation of provincial legislation pertaining to provincial or local protected areas (Section 8).

This Act is of significance to the African penguin since it sets out criteria for the management and regulation of activities on protected areas. Most breeding colonies in South Africa are protected in terms of this Act as they are on areas which have been proclaimed provincial nature reserves or national parks. NEM: PAA provides legislative support to areas which were previously proclaimed under provincial conservation and forestry regulations and this act is specific in the manner in which these areas need to be managed. NEM: PAA acknowledges any previous declaration in terms of the conservation ordinance and forestry legislation and as such, considers those area protected under NEM: PAA.

Chapter 2 describes the system of protected areas in South Africa. In this chapter, the kinds of protected areas are described (Section 9, 12, 13, 15, 16); and a requirement is placed on the Minister to maintain a Register of Protected Areas in Section 10.

Chapter 3 provides more detail on the declaration of protected areas. Section 17 describes the purposes of the declaration of areas as protected areas. In other words, in order for an area to be declared a protected area under this Act, it needs to fulfil purposes that are described in this Act. These include (not all inclusive of what is stated): to protect ecologically viable areas representative of South Africa's biodiversity

in a system of protected areas (17a); to preserve the ecological integrity of those areas (17b); to conserve the biodiversity in those areas (17c); to protect South Africa's threatened or rare species (17e); protect an area which is vulnerable or ecologically sensitive (17f) and to rehabilitate and restore degraded ecosystems and promote the recovery of endangered and vulnerable species. All areas containing breeding colonies of African penguins should be protected under this Act, since they are considered a threatened species under national biodiversity legislation that will be discussed later in this chapter.

Chapter 4 describes the management of protected areas. This chapter deals specifically with those areas that are declared as special nature reserves, nature reserves or protected environments. With the exception of Stony Point, all areas containing African penguin breeding colonies are protected under this Act. This is the chapter which makes provision for the Minister to assign the management of a protected area to a managing authority (Section 38). In addition, it is a legal requirement in terms of this Act, for all protected areas to have a management plan that is submitted to the Minister or MEC for approval within a certain time frame (Section 39). Section 39 also states, that when a protected area management plan is being prepared by the managing authority, the authority concerned must consult with municipalities, other organs of state, local communities and other affected parties which have an interest in the area. This gives all those interested in African penguin conservation the opportunity to be part of the management planning process for the relevant protected areas. Chapter 4 also describes the management criteria by which the managing authority must manage the area (Section 40) and provides detailed instructions as to what the management plan must contain (Section 41). Furthermore, allowance is made for the Minister to establish indicators for monitoring performance with regard to the management of national protected areas, provincial and local protected areas and the conservation of biodiversity in those areas (Section 43). The legislation regarding access to these areas, as well as where access is denied pending the relevant permission and permits, is stated in Sections 45 and 46.

The state is thus required to act as the trustee of protected areas in the Republic at a national, provincial and local level. Table 1 lists the protected areas that contain breeding colonies of African penguins and the relevant managing authority responsible for their management. All protected areas are required to be on the protected areas

register. The submission of the management plans for protected areas is important, since any protected area listed on the register is considered a protected area in terms of the Act. These sites are to be managed in accordance with an integrated management plan that is required to be drawn up for each protected area. These management plans will thus deal with (amongst other aspects): protecting the breeding habitat of this species, mitigating against threats to the African penguin and to conduct relevant monitoring to ensure the management plan is achieving its objectives. The NEM: PAA also states that any relevant Biodiversity Management Plan must be incorporated into the protected area management plan.

When preparing a management plan for a protected area, the management authority concerned must consult municipalities, other organs of state, local communities and other affected parties which have an interest in the area. A procedure for public participation must also be followed, and a Protected Area Advisory Committee is also a requirement under this Act for each protected area. This provides an opportunity for the participation of a range of stakeholders involved in various aspects of African penguin conservation to provide input into the management plan of the various colonies. It also provides the mechanism by which officials from other government departments are able to engage with the managing authority on matters affecting the protected area.

National Environmental Management: Biodiversity Act (NEM: BA) No. 10 of 2004

The National Environmental Management: Biodiversity Act (NEM: BA) (No. 10 of 2004) is drafted under the framework of the National Environmental Management Act described above. NEM: BA is written to: provide for the management and conservation of South Africa's biodiversity within the framework of NEMA; the protection of species and ecosystems that warrant national protection; the sustainable use of indigenous biological resources; the fair and equitable sharing among stakeholders of benefits arising from bio-prospecting involving indigenous biological resources. Additionally, it aims to give effect to ratified international agreements relating to biodiversity which are binding on the Republic; to provide for co-operative governance in biodiversity management and conservation; and to provide for a South African National Biodiversity Institute to assist in achieving the objectives of this Act.

This legislation is binding on all organs of state that implement legislation relevant to biodiversity. They are required to manage, conserve and sustain South Africa's

biodiversity and its components and genetic resources and to implement this Act to achieve the progressive realisation of those rights entrenched in the constitution. These bodies include National authorities primarily the Department of Environmental Affairs, as well as the delegated Provincial Bodies such as CapeNature and Eastern Cape Province to name a few.

A number of chapters within this Act are relevant to this discussion on African penguin conservation and they are briefly highlighted below. Chapter 2 states that the South African Biodiversity Institute (SANBI) is to report to the Minister on the conservation status of all listed threatened or protected species. Chapter 3 deals with biodiversity planning and monitoring and provides for integrated and co-ordinated planning and the preparation of a National Biodiversity Framework (Section 37–48); monitoring the conservation status of various components of South Africa's biodiversity (Section 49) and the promotion of biodiversity research (Section 50). The National Biodiversity Framework must provide for an integrated, co-ordinated and uniform approach to biodiversity management by organs of state in all spheres of government, non-governmental organisations, the private sector, local communities and the public. Under this chapter, allowance is also made for biodiversity management plans (BMP) that can be drafted for indigenous species (BMP-S) or ecosystems, which will be focussed on further in this discussion.

Thus, through its organs that implement legislation applicable to biodiversity, the state must manage, conserve and sustain South Africa's biodiversity, its components and genetic resources and must implement this Act to achieve the above objectives. There is thus a responsibility placed on the State for the protection of the African penguin. The National Biodiversity Framework will need to identify areas for conservation action and the establishment of protected areas. This may involve marine areas that need protection in order to protect the African penguin (and marine biodiversity) through the establishment of a network of offshore marine protected areas. This is a process that SANBI is currently embarking on together with all role players.

Chapter 4 relates to threatened or protected ecosystems and species. The purpose of this chapter is to provide for the protection of ecosystems that are threatened or in need of protection to ensure the maintenance of their ecological integrity (Section 52-55); provide for the protection of species that are threatened or in need of protection to

ensure their survival in the wild (Section 56-58); give effect to the Republic's obligations under international agreements regulating international trade in specimens of endangered species (Section 59–62); and ensure that the utilisation of biodiversity is managed in an ecologically sustainable way.

Chapter 7 deals with the issuing of permits (Section 87-97). Chapter 8 covers the administration of the Act (Section 97–100). Under this chapter, the Minister may make regulations that relate to the following (not all inclusive list): the monitoring of compliance with and enforcement of norms and standards (Section 97 1(a)); the designation of organs of state which may be issuing authorities for permits (b(i)); the facilitation of the implementation and enforcement of an international agreement regulating international trade in specimens of listed threatened or protected species which is binding on the Republic (b(ii)); the minimising of the threat to the survival in the wild of a listed threatened or protected species (b(v)); the designation of organs of state which may be competent authorities for implementing and enforcing the provisions of this Act (c(ii)); the prescription of compulsory conditions for any permit issued in terms of Section 65(1) or 71(1) (c(iii)). Chapter nine covers offences and penalties (Section 101-102).

In terms of Chapter 8 described above, a number of regulations have been gazetted under the Biodiversity Act. Of specific pertinence to the African penguin is the 'Threatened and Protected Species Regulations' (TOPS) which was gazetted on 23 February 2007. The purpose of these regulations include (not all inclusive of what is stated) to: further regulate the permit system set out in Chapter 7 of the Biodiversity Act that relate to restricted activities involving specimens of listed threatened or protected species; provide for the registration of captive breeding operations, commercial exhibition facilities, game farms, nurseries, scientific institutions, sanctuaries and rehabilitation facilities and wildlife traders; provide for the prohibition of specific restricted activities involving specific listed threatened or protected species; provide for the protection of wild populations of listed threatened species; and provide for the composition and operating procedure of the Scientific Authority. The issuing of TOPS permits has been delegated to provincial conservation authorities, and all organisations involved in any of the activities above, need to have a TOPS permit.

The African penguin is listed as "Protected" in terms of Section 56 of the TOPS and it is the intention of the Department of Environmental Affairs (DEA) to align the TOPS status to the Red List status of the IUCN. In terms of these regulations, the following are relevant to the African penguin. Chapter 2 relates to the permit system for listed threatened or protected species. Chapter 3 describes the requirements for the registration of captive breeding operations, commercial exhibition facilities, game farms, scientific institutions, sanctuaries, rehabilitation facilities and wildlife traders. Chapter 4 relates to the renewal, amendment and cancellation of permits and registration certificates. All facilities that perform the functions as defined in these regulations, such as captive breeding, commercial exhibition, scientific institutions and rehabilitation facilities that are involved with African penguins will need to be registered in terms of the TOPS regulations.

In so far as the responsibilities of the state are concerned, with respect to these regulations at a national level, they include the drafting of Norms and Standards for facilities and issuing of permits. At a provincial level, responsibilities include the implementation of the Norms and Standards, inspections and issuing of permits, (including registration with DEA of captive institutions, commercial exhibition facilities and rehabilitation facilities.)

Subsequent to the publishing of the NEM: BA, and its subsequent regulations, The Minister has published Norms and Standards to guide the achievement of the objectives stated within the Acts. Norms and Standards have been gazetted for the compilation of 'Biodiversity Management Plans for Species' (3 March 2009) in terms of Section 9(1)(a)(i) and 43 of the National Environmental Management: Biodiversity Act, 2004 (No. 10 of 2004) (Appendix II). Within these norms and standards, indicators are set in order to measure compliance.

The Act allows for the compilation of the Biodiversity Management Plan for the African penguin. Norms and Standards are provided for the compilation of this management plan that provides criteria for further protection of this species. Under these Norms and Standards, CapeNature and Oceans and Coasts have facilitated the initiation of a Biodiversity Management Plan for the African penguin, the process of which started in March of 2010. Stakeholders were sent a notification of the intent to initiate the development of the BMP-S with a request to indicate their support of this process.

Additionally, stakeholders were requested to furnish details of additional relevant stakeholders that should be included on the stakeholder list which had been attached with the notification. A two and a half day workshop was held in Arniston, in the Western Cape 26–28 October 2010. The aim of the workshop was to identify threats impacting the African penguin population in South Africa and mitigating measures to address them. The proceedings that have arisen from this workshop are currently in the process of being approved (as at January 2011). Once approved, they will then be used to start drafting the African penguin BMP. Agreement on the current content as well as additional content will be sought through a public commenting process, the timelines of which are detailed in the Norms and Standards (Appendix II). Once approved by the Minister (of Environmental Affairs), the African penguin BMP will become a legal document, and those agencies and organisations listed as implementing agents held accountable for the actions required of them in the plan. An annual progress report on the achievement of objectives in the BMP will need to be submitted to the Minister, and the document is to be reviewed every five years.

The BMP, in terms of the framework for which South African national legislation is drafted, cannot contradict existing legislation. Certainly, in compiling the document, a requirement is taking cognisance of other relevant national and provincial legislation. Under the principle of co-operative governance, which all statutory bodies are expected to uphold, and which is one of the cornerstones of the constitution and all subsequent legislation, all acts, ordinance, and legislative instruments are required to take cognisance of other legislation and mandates that exists that may have an impact. The BMP-S for example, while drafted under the National Biodiversity Act, must take into account actions and activities impacting the African penguin. This facilitates greater interaction and transparency amongst all stakeholders, and allows for greater co-operation between government departments, ensuring minimal duplication of efforts. Thus, for example, the work undertaken by the Pelagic Working Group, the Ecosystem Approach to Fisheries and Island Closure task team under DAFF and the MLRA are acknowledged and included as actions within the BMP-S, which is drafted under National legislation of a different Minister.

Knight *et al.* (2008) conducted a literature survey on published conservation assessments and subsequently, based on a questionnaire sent to the authors of these assessments, quantified how many of these assessments could report conservation

implementation. They found that only 5.7% of the respondents documented the implementation of actions that promoted nature conservation on the ground. Furthermore, only 26% of the conservation assessments had the objective of implementing some form of action. For the purposes of their survey, Knight *et al*. (2008) defined conservation assessment as any spatially explicit, repeatable approach that identifies areas as potential priorities for nature conservation activities. While the BMP-S does not fall strictly within their definition, the conclusions drawn and recommendations made have direct bearing on the value of the BMP process. Knight *et al*. (2008) conclude that the majority of the conservation assessments published were not designed with the intention to implement conservation action. Furthermore, they recommend that conservation assessments should be linked to implementation strategies that detail the actions required to for achieving conservation goals. A requirement of the BMP-S for the African penguin is that it contains an implementation plan that includes an action plan, with identified implementers and associated time frames. The BMP-S is incomplete without it, and will not be approved by the Minister. Furthermore, the Minister will require an annual report of implementation. This highlights the strength of what the BMP-S can achieve in terms of achieving actions required for the biodiversity conservation of a species.

One of the recommendations made by Knight *et al*. (2008) is that research questions should be sourced from practitioners. Furthermore, Knight *et al*. (2008) stated the need for institutions to translate science into action by fostering relationships between researchers and practitioners. The workshop in October 2010 (minutes of this meeting to be formally adopted in March 2011) was attended by scientists, practitioners, other government representatives and a number of NGOs. It therefore facilitated the type of interaction suggested above.

The BMP-S for the African penguin can thus be considered an effective tool for conservation implementation since it has an action plan attached, which identifies implementation actions, implementers and time frames which becomes a legally binding document. This BMP-S is also required to be adopted and integrated into the management plans of the relevant protected areas. It is drafted under the NEMA principles, and so co-operative governance is core to its implementation. This should start to address the lack of cohesion and communication between the government departments involved in aspects of this BMP-S.

Thus, in as much as it makes provision for the execution of all actions identified for the protection and conservation of the African penguin, it is considered the most effective tool to legislate biodiversity conservation for this species in South Africa.

PROVINCIAL LEGISLATION

For the purposes of this discussion, the Western Cape Nature Conservation Board will be used as an example of a provincial conservation body.

CapeNature is an organ of state as it is a statutory body in the provincial sphere of government, exercising a public power and performing a public function in terms of relevant legislation (Smith 2005). CapeNature's area of jurisdiction is limited to the Western Cape Province. The role of CapeNature in terms of regulating activities which have an impact on the environment, as well as for the protection of the environment is within the provisions of the Constitution, other environmental legislation such as NEMA discussed above, and specific legislation that pertain directly to CapeNature itself, such as the Western Cape Provincial laws (Smith 2005).

In terms of the Constitution, CapeNature, as an organ of state, is required to adhere to the principles of co-operative governance, that are specified in Chapter 3 of the Constitution, at all times (Smith 2005). Furthermore, all decision making by CapeNature must be consistent with the constitutional environmental right, contained in the Bill of Rights. The Bill of Rights applies between the State and Citizen (Section 8(1)). If any person feels that CapeNature (or any organ of state for that matter) is violating this right, or failing to protect it, they can enforce this right through the courts against the relevant organ of state.

The Western Cape Nature Conservation Board Act No. 15 of 1998

The Western Cape Nature Conservation Board Act No. 15 of 1998 establishes the Western Cape Nature Conservation Board (CapeNature 2005). The objectives of this Act are to: promote and ensure nature conservation and related powers in the Western Cape Province; render services and provide facilities for research and training in connection with nature conservation and related matters in the province.

CapeNature operates under the Western Cape: Nature and Environmental Conservation Ordinance 19 of 1974 which regulates nature and environmental conservation in the province. This ordinance assigns a provincial threat status to the African penguin. Section IV deals with the protection of wild animals other than fish. Under this Section, Schedule one lists species which are considered endangered wild animals within the province, under which the African penguin is listed.

The definition of an endangered species in the ordinance is as follows: a wild animal of any species which is in danger of extinction and is specified in Schedule I or Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora, Washington, 1973; provided that it shall not include a wild animal of any species specified in such Appendix and Schedule 2.

CapeNature has a dual role of regulating activities which have an effect on the environment, as well as a role in protecting the environment as a managing authority for protected areas. These authorities are provided for under the provisions in the Constitution, environmental legislation (such as the NEM Acts detailed in this document) and other specific legislation such as the Western Cape Nature Board Act and the Western Cape Nature Amendment Act.

CapeNature manages provincial nature reserves, and in the context of the African penguin, this includes Dassen Island and Dyer Island. CapeNature is currently (2011) involved in negotiations with the Overstrand Municipality to ensure that the Stony Point colony be gazetted as a CapeNature Stewardship site, affording it the same protection status as a Provincial Nature Reserve. All three areas, Dassen Island, Dyer Island and Stony Point will require management plans in terms of the NEM: PAA. As part of the management plan process, a protected area advisory committee will need to be established for each area, thereby facilitating stakeholder engagement into the management of these areas.

CapeNature is also responsible for the issuing of permits which regulate any restricted or prohibited activity. These include research permits for any research within the boundaries of the Western Cape province (except within the boundaries of South African National Parks). CapeNature also comments new and updated regulations and policies.

FINAL COMMENTS

The current legislative framework in South Africa (as at February 2011) pertaining to environmental and specifically biodiversity conservation is considered adequate for the conservation of this species. The approach to the conservation of this species is however fragmented, and the development of the BMP-S aims to unite conservation efforts. It is recommended that all African penguin breeding colony sites be proclaimed protected areas in terms of NEM: PAA. This is particularly relevant to the Stony Point colony within the jurisdiction of the Overstrand Municipality. Furthermore, all managing authorities should take responsibility to ensure that their information is verified on the Protected Areas Register, which as it stands in February 2011 is outdated.

When the BMP-S is gazetted, I recommend that all management authorities of African penguin breeding colonies amend their protected area management plans to ensure that they incorporate the BMP–Ss actions into their protected area management plans. Furthermore, all management and regulatory authorities (including other government agencies and departments) should build capacity towards the implementation and understanding of the legal framework towards the conservation of the African penguin.

The Department of Environmental Affairs should develop a clear communication strategy for public dissemination regarding the issuing authorities and responsibilities for TOPS permits.

With respect to all African penguin stakeholders, including those outside of the formal legislative bodies, it is important to know the legislative context for the protection of this species. Under the NEMA principles, organisations that are not management or regulatory authorities, have a scrutiny responsibility, in other words, a duty of care.

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Seal and Seabirds Act, No. 46 of 1973

Seal and Seabirds Policy, Notice 1717 of 2007

Western Cape Nature Conservation Laws Amendment Act, No. 3 of 2000

Western Cape Nature Conservation Board Act, No. 15 of 1988

Table 1: The managing authorities of African penguin colonies in South Africa

COLONY	MANAGING AUTHORITY	PROTECTED AREA STATUS	DATE PROCLAIMED	CAPTURED ON PROTECTED AREA REGISTER
Lambert's Bay Penguin Island	CapeNature	Provincial Nature Reserve	9 March 1988	Yes
Malgas Island	SANParks	National Park, Marine Protected Area		No
Marcus Island	SANParks	National Park, Marine Protected Area		No
Jutten Island	SANParks	National Park, Marine Protected Area		No
Vondeling Island	CapeNature	Provincial Nature Reserve	9 March 1988	No
Dassen Island	CapeNature	Provincial Nature Reserve	9 March 1988	Yes
Robben Island	Robben Island Museum (Department of Arts and Culture)	Robben Island Museum (1997). World Heritage Site (1999). National Heritage Site (2006)	Robben Island Museum (1997). World Heritage Site (1999). National Heritage Site (2006)	No
Boulders	SANParks	National Park TMNP MPA 2004	National Park TMNP MPA 2004	No
False Bay – Seal Island	CapeNature	Provincial Nature Reserve	9 March 1988	Yes
Stony Point	Overstrand Municipality	Municipal Public Open Space		–
Dyer Island	CapeNature	Provincial Nature Reserve	9 March 1988	Yes
Geyser Island	CapeNature	Provincial Nature Reserve	9 March 1988	Yes
De Hoop Marine Reserve	CapeNature	Marine Protected Area (1985)	Marine Protected Area (1985)	Yes
Jahleel Island	SANParks	National Park		No
Brenton Island	SANParks	National Park		No
St Croix Island	SANParks	National Park		No
Seal Island - Algoa Bay	SANParks	Bird Island MPA (2004) and Addo Elephant National Park (2005)	Bird Island MPA (2004) and Addo Elephant National Park (2005)	No
Stag	SANParks	Bird Island MPA (2004) and Addo Elephant National Park (2005)	Bird Island MPA (2004) and Addo Elephant National Park (2005)	No
Bird Island - Algoa Bay	SANParks	Bird Island MPA (2004) and Addo Elephant National Park (2005)	Bird Island MPA (2004) and Addo Elephant National Park (2005)	No

Appendix I: International conventions and agreements to which South Africa is signatory to.

1) Convention on Biological Diversity

The Convention on Biological Diversity was inspired out of the world community's 'growing commitment to sustainable development taking cognisance that threats to species and ecosystems have never been so great as they are today, and that species extinction caused by human activities continue at an alarming rate.'

In response to these concerns, the United Nations Environment Programme (UNEP) convened an Ad Hoc Working Group of Experts on Biological Diversity in November 1988 to explore the need for an international convention on biological diversity.

After a process of five years, the Convention entered into force on 29 December 1993. The first session of the Conference of the Parties was held in 1994 in the Bahamas. The Convention on Biological Diversity (CBD) has three main objectives: i) the conservation of biological diversity; ii) the sustainable use of the components of biological diversity; iii) the fair and equitable sharing of the benefits arising out of the utilization of genetic resources.
(source: http://www.cbd.int/convention/about.shtml)

Once ratified, a signatory (country) is required to incorporate the principles of the convention into their national Legislation, which South Africa has done through the National Biodiversity Act.

2) International Union for the Conservation of Nature (IUCN)

The IUCN's Red List is a mechanism for evaluating the conservation status of a species. The goals of the Red List are to: identify and document those species most in need of conservation attention if global extinction rates are to be reduced; provide a global index of the state of change of biodiversity and provide an internationally recognised standard of describing the conservation status of a species.

In 2010, the IUCN Red List category (as evaluated by BirdLife International - the official Red List Authority for birds for IUCN) for the African penguin changed from 'Vulnerable' to 'Endangered.' The justification provided for this was because "recent

data has revealed that it is undergoing a very rapid population decline, probably as a result of commercial fisheries and shifts in prey populations. This trend currently shows no sign of reversing, and immediate conservation action is required to prevent further declines."
(source: http://www.iucnredlist.org/apps/redlist/details/144810/0)

This status identifies the African penguin as a species requiring immediate conservation action, and is thus a tool for conservation agencies (government and NGO, NPO) to guide where capacity and funding need to be focussed.

3) Convention of Migratory Species of Wild Animals (CMS) or Bonn Convention
The Convention on the Conservation of Migratory Species of Wild Animals (also known as CMS or Bonn Convention) aims to conserve terrestrial, marine and avian migratory species throughout their range. It is an intergovernmental treaty, concluded under the auspices of the United Nations Environment Programme, concerned with the conservation of wildlife and habitats on a global scale. The convention entered into force in 1979.

Convention listed species are assigned to different categories according to set criteria.
Appendix 1: Endangered migratory species. The conventions has set criteria for how these species are managed to which all parties need to comply.
Appendix 2: Migratory species that have an unfavourable conservation status or would significantly benefit from international co-operation are listed in Appendix II of the Convention. For this reason, the Convention encourages the Range States to conclude global or regional agreements for the conservation and management of individual species or, more often, of a group of species listed on Appendix II.

In this respect, CMS acts as a framework convention from which independent instruments evolve. The Agreements may range from legally binding treaties to less formal instruments, such as Memoranda of Understanding, and can be adapted to the requirements of particular regions. The development of models tailored according to the conservation needs throughout the migratory range is a unique capacity of CMS.

Such agreements have the great advantage that the Range States themselves decide on a tailored and structured action plan that includes the organization of joint research, monitoring activities and harmonisation of legislation.

South Africa is signatory to the Bonn Convention (1 Dec 1991) and is signatory to two agreements under the Convention:
AEWA: Agreement on the Conservation of African-Eurasian Migratory Waterbirds (1 November 1999)
ACAP: Agreement on the Conservation of Albatrosses and Petrels (1 February 2004)
(Source: http://www.cms.int/about/intro.htm)

The African penguin is listed in Appendix II (COP5). There is as yet no international agreement between governments for this species. Should such an agreement take place, it would include Angola, Namibia, South Africa, Mozambique.

4) Convention on International Trade in Endangered Species of Wild Fauna And Flora (CITES)

CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora) is an international agreement between governments. Its aim is to ensure that the international trade in specimens of wild animals and plants does not threaten their survival in the wild. States (countries) adhere voluntarily to the agreement. States that are signatories to the Convention are known as Parties. Although CITES is legally binding on the Parties, that is, they have to implement the provisions of the Convention, it does not take the place of national laws. Rather it provides a framework to be respected by each Party, which in turn have to adopt its own domestic national legislation to ensure that CITES is implemented at the national level. The CITES regulations are included in the South African legislation through the National Environmental Management: Biodiversity Act (No. 10 of 2004).

CITES lists species in appendices, based on certain criteria. Appendix II (in which the African penguin is listed) lists species that are not necessarily now threatened with extinction but that may become so unless trade is closely controlled. International trade in specimens of Appendix-II species may be authorized by the granting of an export permit or re-export certificate. No import permit is necessary for these species under CITES (although a permit is needed in some countries that have taken stricter

measures than CITES requires). Permits or certificates should only be granted if the relevant authorities are satisfied that certain conditions are met, above all that trade will not be detrimental to the survival of the species in the wild.
(source: http://www.cites.org/eng/disc/what.shtml)

South Africa's inclusion in CITES was ratified on the 15 July 1975, and it came into force on the 13 October 1975. The Department of Environmental Affairs (DEA) is the South African national management authority for CITES. DEA has in turn designated provincial conservation authorities as provincial management authorities. CapeNature has such delegated authority for CITES listed species within the Western Cape province. African penguins cannot be sold to an international body and transported to international destinations without a CITES permit that is issued by DEAT or a delegated authority.

Appendix II: Norms and Standards for the compilation of Biodiversity Management Plans for species, which are drafted under the National Environmental Management: Biodiversity Act (No. 10 of 2004).

CHAPTER 7

SYNTHESIS

Photo: D. Geldenhuys

SYNTHESIS

Thesis summary

The Benguela Upwelling Ecosystem is one of the most productive ocean systems in the world (Brown *et al*. 1991), but has undergone considerable variation and degradation in the last century such that a long term decrease in fish catches and ecosystem degradation has occurred over large portions of the Benguela Current Large Marine Ecosystem (BCLME) (BCLME Executive Summary 2007). The BCLME (BCLME) Programme aimed to assess the effectiveness of using marine top predators as biological indicators of further ecosystem change in the BCLME and to implement an appropriate, integrated, system wide monitoring programme to support sustainable management of the BCLME (BCLME Executive Summary 2007).

The fieldwork for the project centred around Dyer Island, a Provincial Nature Reserve managed by CapeNature, the Western Cape provincial conservation authority. While long term datasets are available for some seabird species, these are primarily focused on moult and active nest counts of African penguins, and active nest counts of a number of other breeding seabirds such as Cape, White-breasted, Bank and Crowned Cormorants, Swift Terns, Kelp and Hartlaub's gulls as well as African Black oystercatchers. However, in order to fully understand how these top predators are interacting with their environment, a more focused monitoring programme needs to be put in place as recommended by Kemper (2007), ensuring that it is sustainable, and able to be continued on a long-term basis.

In addition to the monitoring recommendations set by the BCLME (Kemper 2007), the fishery closure project also formed an important backdrop to this study. The focus of thes closures were on Dassen Island and Robben Island (2008 and 2009) and St Croix Island and Bird Island (2009 and 2010). Data provided in this study will provide a reference point against which effects of any future fishery related management actions can be measured.

Key Research findings

African penguin interaction with pelagic fish

African penguin colonies have been shown to exhibit regional coherence in terms of their population trends (Underhill *et al*. 2006). That Dassen Island and Robben Island are only 50 km apart suggests that these two islands experience similar oceanographic

environments. Results in this study showed that African penguins on these two islands exhibited different responses to the fish models. These results suggest that feeding conditions are not similar around these two islands. Additionally, the ability of African penguins to provision sufficiently for the moult period is considered of paramount importance to the survival of this species. The strongest modelled relationships were those with the African penguin population estimates and the spawner biomass of the previous year, suggesting that survival and post-moult condition is a strong determinant of breeding numbers for the following year. This factor is important to consider when accounting for food requirements in future Ecosystem Approach to Fishery modelling approaches.

Adult moult phenology

The results of this chapter confirm findings in Chapter 2. Moult patterns obtained from Namibia and South Africa suggests that there is substantial movement of moulting African penguins away from breeding locations to other localities to moult. The proportion of breeders to non breeders reflects a combination of recruitment, mortality, and breeding conditions for a year, and will not be constant (Kemper *et al*. 2008). The ratio of breeders to adult moulters was not constant throughout all the colonies, with a declining trend. This may have been caused by an increase in non-breeders in the populations. However, given the associated decline in overall population numbers, this is unlikely to be the case.

African penguin chick condition

The condition index developed by Lubbe (2008) provides a tool to assess chick condition for samples of chicks of unknown ages, of different sizes, and allows for spatial and temporal comparisons to be made. There was significant spatial and temporal variability in chick condition, between years, across months and between successive sampling dates. The variability within colonies suggests that colonies do not respond uniformly with temporal differences in peak condition between Dassen Island and Robben Islands, only 50km apart for example, being observed. There was also evidence of decreasing chick condition over time, with 2009 being poorer overall than that of 2008, with both years being poorer than 2004. This suggests that feeding conditions have deteriorated over time. The condition index can thus be considered a useful indicator of feeding conditions over periods of about two weeks.

The chick condition index does not rely on chicks of known age, or that chicks of known identity be followed through to fledging as would be the case in studies of chick growth rates. This technique does not require the use of expensive equipment and it so it is considered a useful tool to adopt as a standard monitoring practise that can be included in all African penguin breeding colony monitoring programmes.

Foraging

There was no significant difference in trip duration, foraging range and distance travelled between years, suggesting that foraging effort around Dyer Island remained the same during the course of the study. It is acknowledged however that the sample sizes in this study are small. Mean depth and mean foraging depth as well as bottom time duration, mean foraging duration and foraging efficiency differed between years. This is likely attributable to the shallower area that the birds were foraging in during 2010.

In comparison with foraging studies of breeding African penguins at other colonies, results of this study suggest that African penguins at Dyer Island worked harder for their food, with longer trip durations, larger foraging ranges, larger total distance travelled recorded in this study than at other studies.

Legislation

The legislative framework within South Africa is considered adequate for biodiversity conservation for an endangered species such as the African penguin. It is however not being implemented effectively. Environmental legislation is structured within the framework of the National Environmental Management Act (No. 107 of 1998) which includes principles of co-operative governance. There is not enough interaction between government departments at the various tiers of government to ensure best management practises for the conservation of this species are adopted.

The Biodiversity Management Plan for the African penguin, which is being drafted under the National Environmental Management Act (No. 10 of 2004) is considered an effective means by which to compile a conservation assessment and action plan for this species. The approach followed thus far toward developing this plan has been one of considerable stakeholder participation and engagement. Part of this process is ensuring that all stakeholders, including those outside of the legally mandated bodies, are aware and understand the legislative context for the protection of this species. By so doing,

scientists can design their research programmes accordingly, and NGOS can align their programmes to best assist government in achieving the conservation of this species. Not only that, but it creates a means by which non-government stakeholders can assess government compliance and implementation of the plan, ensuring public accountability.

Future research directions

African penguin interaction with pelagic fish

Predator prey dynamics of African penguins to surrounding fish stocks needs more in depth research. Part of this will entail a deeper understanding of the temporal and spatial movement of prey at a finer scale than the biomass surveys are currently conducted. This is especially true during the pre-moult fattening and post moult recovery phase of the African penguins which .

Moult

The relationship to moult timing and breeding patterns requires further analysis, particularly at Dyer Island where breeding success studies have not been conducted since the mid 1980s. This work is currently underway. A comparison of timing of breeding and moulting between all the colonies in South Africa will then be possible, which will provide further insights as to how the African penguins at the various colonies are responding to their environments, and if there are colony specific patterns that are apparent.

Immature survival is a key component in understanding population dynamics of long-lived seabirds, including the African penguin (Kemper and Roux 2005). An updated assessment of juvenile moult patterns in South Africa is required, since this will provide an indication to the recruitment of adults into the population. Juvenile African penguins are highly mobile, not necessarily restricted to return to the colony from which they fledged. They have the flexibility to move from their natal colony to where feeding conditions are more favourable (Crawford *et al*. 2000), which will provide further information on the availability of food. The interpretation of immature moult counts may not be accurate for individual colonies but will be valid at a regional scale.

The need for banding of African penguins to continue in South Africa also needs to be highlighted, since the interpretation of movement patterns, juvenile and adult survival rely on this information. Information obtained from banding will also aid in determining the proportion of breeders that defer breeding, an aspect that is important

for ensuring accurate assessments and causes of breeding deferment. The development of suitable bands must be considered high priority in South Africa in 2011.

Chick condition

The relationship of chick condition to the catch data would be a useful avenue to pursue, since fish catch data can be considered a proxy for fish availability in the area.

It is questionable whether chicks below the 5% quantile line, i.e. with a condition index below 0 are able to recover and fledge successfully (Lubbe 2008). The next phase in this study will be to monitor the condition of 'known' chicks in attempt to estimate a 'starvation line' (Lubbe 2008). An established conservation intervention for African penguins is the removal of abandoned, end of season chicks to be hand-reared and released (Parsons and Underhill 2005, Parsons *et al*. 2007, Barham *et al*. 2008). It would be useful to know what the lowest level of chick condition can be reached before for a chick should be removed for hand rearing, since the artificial raising of chicks is considered an important conservation intervention for a rapidly declining endangered species.

Foraging

Determining the foraging area during the pre-moult fattening and post-moult recovery is of crucial importance in understanding adult moult survival. A joint study investigating the foraging behaviour of African penguins with Cape Cormorants, seals and sharks during the penguin breeding season may provide some insights into the overlapping foraging area of these species, and some understanding of the predation threat to foraging penguins at sea.

An investigation of the relationship of penguin foraging behaviour to fishing activity within the foraging range of penguins is an important future direction. This will aid in determining what impact fishing activity has on penguin foraging behaviour.

The need for small-scale surveys of fish distribution and abundance around colonies, timed to coincide with logger deployment, would be valuable in understanding foraging behaviour in relationship to dynamic and unpredictable food sources. Both logger deployment and fish surveys are however expensive. Research should also focus on whether monitoring of chick growth rate (Sherley 2010) and chick condition indices

(Chapter 4) are more easily measured surrogate variables, able to provide insights into the quality and quantity of food available to adults foraging around breeding colonies.

Although Dyer Island lies along the same population of anchovy on passage past Dassen Island, Robben Island, and Boulders, food seems to be scarcest for the penguins breeding at Dyer Island. This could be due to fishing pressure, or related to other factors such as predation, where staying away longer from the island reduces the risk of being eaten by seals, or, more likely a combination of factors. Differences in foraging behaviour may not be completely explained by prey availability and other factors may also need to be considered such as the threat of predation and spatial dynamics of shoals. There is a need for ongoing foraging studies to understand birds' response to changing, dynamic environment.

Legislation

One of the keys to ensuring the success of the Biodiversity Management Plan for the African penguin is to constantly evaluate the level of implementation, and whether the activities that are being implemented are having measurable effect. In order to do this, an evaluation tool is needed. Furthermore, an assessment will need to be made as to whether the indices used to assess success of the plan are the most effective ones to use.

An important aspect of the success of the plan is the level of stakeholder involvement, and knowledge and understanding of the legislative framework within which it is placed. A means of quantifying and assessing the level of stakeholder engagement would be valuable for this and future Biodiversity Management Plans for species.

Concluding remarks

Dyer Island and Stony Point are c. 60 km apart. The colonies have, however, exhibited different population trends. Similarly, the population trend at Dyer Island, the largest African penguin colony in the late 1970s, has been different to that of other colonies such as Dassen Island and Robben Island. During the course of this study, chicks at Dyer Island had the poorest condition of all colonies, and the penguin's foraging range and trip duration were longer than that observed at other colonies. Understanding the population dynamics at Stony Point may provide insight as to why the penguins on Dyer Island, since 1970, have a decreasing trend.

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GOVERNMENT NOTICE

DEPARTMENT OF ENVIRONMENTAL AFFAIRS AND TOURISM

No. R. 214 **3 March 2009**

NATIONAL ENVIRONMENTAL MANAGEMENT: BIODIVERSITY ACT, 2004 (ACT 10 OF 2004)

NORMS AND STANDARDS FOR BIODIVERSITY MANAGEMENT PLANS FOR SPECIES

I, Marthinus Christoffel Johannes van Schalkwyk, Minister of Environmental Affairs and Tourism, hereby publish the Norms and Standards for Biodiversity Management Plans for Species in terms of section 9(1)(a)(i) and 43 of the National Environmental Management: Biodiversity Act, 2004 (Act no 10 of 2004), as contained in the Schedule.

Signed by candidate

MARTHINUS VAN SCHALKWYK
MINISTER OF ENVIRONMENTAL AFFAIRS AND TOURISM

SCHEDULE

TABLE OF CONTENTS

ACRONYMS

AEWA	African Eurasian Migratory Waterfowl Agreement
BMP	Biodiversity Management Plan
BMP-S	Biodiversity Management Plan for species
CBD	Convention on Biological Diversity
CITES	Convention on the International Trade in Endangered Species of Fauna and Flora
DEAT	Department of Environmental Affairs and Tourism
IDP	Integrated Development Plans
IUCN	World Conservation Union
MOA	Memorandum of Agreement
NEM: BA	National Environmental Management: Biodiversity Act (Act No. 10 of 2004)
NBF	National Biodiversity Framework
NEMA	National Environmental Management Act (Act No. 107 of 1998)

CHAPTER 1
INTERPRETATION AND THE PURPOSE OF THESE NORMS AND STANDARDS

Definitions

1. (1) In these Norms and Standards, unless the context indicates otherwise, a word or expression defined in the Biodiversity Act or Protected Areas Act has the same meaning, and—

"Biological diversity or biodiversity" means the variability among living organisms from all sources including, terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part and also includes diversity within species, between species, and of ecosystems.

"Ex-situ or 'off-site' conservation" means the conservation of genetic resources and of wild animals, plants, fungi and microorganisms off-site or outside their natural habitats.

"Indigenous species" means a species that occurs, or has historically occurred, naturally in a free state in nature within the borders of the Republic, but excludes a species that has been introduced in the Republic as a result of human activity.

"In-situ - "on-site" conservation" means the conservation of biodiversity in the wild through the conservation of ecosystems and natural habitats, and the maintenance and recovery of viable populations of species in their natural surroundings.

"IUCN Red Data List" means a global or national list providing information on a species' risk of extinction (usually by taxonomic group), and prepared under the auspices of the International Union for the Conservation of Nature.

"Long-term survival" means to ensure the survival of a species until the next human generation, approximately 30 years.

"Migratory species" means an entire population or any geographically separate part of the population of any species or lower tax on of wild animals, a significant proportion of whose members cyclically and predictably cross one or more national jurisdictional boundaries.

"Stakeholder" means a natural or juristic person(s) that has an interest in, or may be affected by, a particular obligation or decision or activity, relating to or resulting from a management plan, either as individuals or representatives of a group, and include landowners where appropriate.

"Species" means a kind of animal, plant or other organism that does not normally interbreed with individuals of another kind, and includes any sub-species, cultivar, variety, geographic race, strain, hybrid or geographically separate population.

"Threat" means any action that causes a decline and compromises the future survival of a species or anything that has a detrimental effect on a species. Threats can be human induced or natural. BMP-S should focus on mitigating human induced threats to species.

"Viable" in relation to a species or population means the ability to survive or persist and develop or multiply over multiple generations or a long time period.

(2) In this document, unless the context indicates otherwise, a word or expression to which a meaning has been assigned in the National Environmental Management: Biodiversity Act, 2004 (Act No. 10 of 2004), (hereinafter "The Act"), has the same meaning.

Purpose and application

2. (1) In terms of Section 9(1) of the Biodiversity Act, the Minister may, by notice in the *Gazette*—

(a) issue norms and standards for the achievement of any of the objectives of this Act, including for the -

(i) management and conservation of South Africa's biological diversity and its components;

(ii) restriction of activities which impact on biodiversity and its components; and

(b) set indicators to measure compliance with those norms and standards.

(2) The purpose of these Norms and Standards is to provide a national approach and minimum standards for the development of biodiversity management plans for species.

CHAPTER 2
INTRODUCTION TO BIODIVERSITY MANAGEMENT PLANS FOR SPECIES AND TO THESE NORMS AND STANDARDS

Biodiversity Management Plans

3. (1) A biodiversity management plan must –

(a) be aimed at ensuring the long-term survival in nature of the species to which the plan relates;

(b) provide for the responsible person, organisation or organ of state to monitor and report on progress with implementation of the plan; and

(c) be consistent with –

(i) The Act;

(ii) The national environmental management principles;

(iii) The national biodiversity framework;

(iv) Any applicable bioregional plan;

(v) Any plans issued in terms of Chapter 3 of the NEMA;

(vi) Any municipal integrated development plans;

(vii) Any other plans prepared in terms of national or provincial legislation that is affected; or

(viii) Any relevant international agreements binding on the Republic.

(2) Biodiversity Management Plans for Species (BMP-S) can be compiled for any indigenous or migratory species to South Africa.

CHAPTER 3
THE DEVELOPMENT OF BIODIVERSITY MANAGEMENT PLANS FOR SPECIES

Scope of BMP-S

4. Depending on the biological characteristics of the species concerned and the geographic range where it applies, biodiversity management plans may be developed for:

(1) One or more species; or

(2) One or more populations or a meta-population.

Process for developing BMP-S

5. The following process as outlined herein may be followed when developing BMP-S:

(1) Appropriate stakeholders should be invited to participate in the development of the BMP-S.

(2) Stakeholders may be identified according to:

(a) The stakeholder group to which they belong; or

(b) Their interests and mission.

(3) Background information on the species may be compiled and circulated to all appropriate stakeholders prior to development of the BMP-S.

(4) The background information should contain:

(a) Criteria used to select the species;

(b) Information on the current status of the species;

(c) Information on known threats; and

(d) Their impacts on the species.

(5) Compilation of the first draft of a BMP-S can be done by either:

(a) A consultant;

(b) An expert on the species;

(c) A panel of experts on the species; or

(d) During a stakeholder workshop.

(6) (a) The first draft of the BMP should be made available to stakeholders for comment;

(b) The comment period should be at least 30 working days;

(c) Relevant comments received should be included in a final draft of the BMP-S;

(7) The final draft of the plan should be sent to all implementers of identified actions for validation within 60 days of date of notice.

The final draft of the plan should be compiled and submitted, within 90 days of receipt of comments, to the Minister for approval.

Format of BMP-S

6. Title, Table of Contents and Terms

(1) BMP-S must contain the following introductory information:

(a) A header page containing BMP-S title, authors, lead agency and implementing organisations;

(b) A Table of Contents page;

(c) A list explaining abbreviations;

(d) A list of explaining acronyms;

(e) A glossary defining all scientific and technical terms used in the BMP-S in alphabetical order;

(f) Acknowledgements;

(g) Foreword; and

(h) An executive summary in English.

(2) In the BMP-S the introduction must contain:

(a) A brief introduction of the species and why it needs a BMP-S;

(b) Aims and objectives of the BMP-S, which should be a statement of a desired state the plan intends to achieve at the end of its implementation;

(c) Benefits of the plan; and

(d) Anticipated outcomes.

(3) In the BMP-S the background may include:

(a) A Summary of the conservation status and legislative context;

(b) A Summary of everything known about the species and anything pertinent to its management, in sufficient detail, including identified needs to be researched;

(c) Identify role players; and

(d) Summarise planning methodology.

(4) In the BMP-S the conservation status and legislative context may:

(a) Identify parties currently responsible for management of the species for which the BMP-S is developed;

(b) Indicate the status of the species in terms of the Act, IUCN Red Data List, CITES, other national legislation or subordinate legislation and provincial conservation legislation and ordinances;

(c) Indicate the cultural conservation status of the species;

(d) Indicate the indigenous knowledge value of the species; and

(e) Motivate for assigning priority for the development of this BMP-S.

(5) In the BMP-S the species detail may include:

(a) Taxonomy, including sub-specific and genetic information, if relevant and available;

(b) Distribution, migratory patterns (if applicable), habitat requirements, biology and ecology;

(c) Description and map of geographic area for which the plan is proposed;
(d) Any *ex situ* populations and their status;
(e) If known, the species' role in the ecosystem *e.g.* umbrella, keystone, flagship, mutualisms and dependencies;
(f) Known diseases;
(g) Population statistics and trends;
(h) Threats;
(i) Information on any utilisation, where applicable, should include:
    (i) Impact of utilisation based on evidence;
    (ii) Use value of the species;
    (iii) Monitoring of current use; and
    (iv) Current quotas and permits issued;
(j) Past conservation measures;
(k) Socio-economic issues (if applicable), including:
    (i) Community benefits; and
    (ii) A cost analysis of the value of species; and
(l) Research inventory and summary;

(6) In the BMP-S the summary of the planning methodology may include:
(a) A list of role players and organisations involved in developing and implementing the BMP-S;
(b) A description of the processes followed in drawing up the BMP-S;
(c) An outline of the process followed for stakeholder consultation;
(d) A list of all stakeholders;
(e) An outline of the nature of agreements that will need to be or have been developed with implementers of the BMP-S;
(f) Reference to all relevant documents, agreements and policies, which will be appended to the BMP-S; and
(g) Verification and approval by relevant experts on the quality and context of the species related issues.

(7) In the BMP-S the statement of threats adversely affecting the species may include:

(a) List all the threats;

(b) A Description of the nature of the threats including an assessment of the magnitude and impact of the threat; and

(c) Prioritise the threats.

(8) (a) In the BMP-S the action plan stating the objectives and actions for dealing with each of the threats adversely affecting the species should be developed.

(b) Actions identified in an action plan may be divided into actions at the national and local level for ease of reference by implementers, including organs of state at different levels.

(c) The action plan may:

(i) Describe the objectives;

(ii) Describe the action(s) needed;

(iii) Rank each action by relative priority;

(iv) Identify the implementing party(ies), and the lead party;

(v) Specify time frames (initiation, duration, completion date);

(vi) Identify resources needed and outline a resource mobilization strategy to ensure acquisition and sustainability of resource requirements;

(vii) Identify potential positive and negative impacts of action;

(viii) Identify incentives (where applicable);

(ix) Develop measurable indicators; and

(x) List inappropriate actions and explain why they could be detrimental

(9) (a) In the BMP-S a monitoring programme may be developed and may include a monitoring and reporting plan with annual reports for each action outlined in the Action Plan.

(b) For each action, the annual report may include:

(i) A list of the agency(ies) responsible for monitoring each action (this may differ from the implementing or lead agent); and,

(ii) Stipulated milestones, key events and thresholds in the measurable indicators to be reported on.

(10) In the BMP-S the reference list must include all references sited in the BMP-S developed.

Approval of the BMP-S

7 (1) The BMP-S must be submitted to the Minister for approval.

(2) The Minister should, within 90 days:

(a) Acknowledge receipt of a BMP-S;

(b) In the event of an acceptable first draft of a BMP-S, reject, return for revision or publish a BMP-S for general public consultation;

(c) Reject the redrafted version of any BMP-S that does not comply with the norms and standards; or

(d) On approval of a BMP-S the Minister should appoint a lead agency and publish the BMP-S in the Government Gazette.

(3) (a) Before approving a draft biodiversity management plan, the Minister must identify a suitable person, organisation or organ of state that is willing to be responsible for the implementation of the plan.

(b) The Minister may, require independently obtained proof of the lead agency's:

(i) Relevant experience; and

(ii) Financial and human resources.

(c) The Minister may enter into a biodiversity management agreement with the person, organisation or organ of state regarding the implementation of the biodiversity management plan, or any aspect thereof.

Implementation of BMP-S for species

8. (1) The Minister may review, assess compliance and verify achievement of the aim and objectives of a BMP-S;

(2) The Minister may:

(a) Assess compliance and achievement of the aims and objectives as per the monitoring section of the annual reports;

(b) Request any additional information to allow the assessment of compliance and achievement of the aims and objectives, and

(c) The Minister must review a BMP-S published in terms of section 43(3) of the Act, at least every five years, and assess compliance with the plan and the extent to which its objectives are being met.

(3) (a) An annual progress report on implementation of a BMP-S must be submitted to the Minister.

(b) The annual report must include:

(i) A brief introduction;

(ii) Report on progress on each action as contained in the BMP-S;

(iii) Identify problems, bottlenecks, impediments to achieving any action or part thereof; and

(iv) Report on progress towards achievement of objectives contained in the BMP-S.

(4) The Minister may after considering the BMP-S annual report:

(a) Acknowledge satisfactory acceptance thereof;

(b) Request further clarification on any action that is not adequately reviewed in the report;

(c) Appoint an advisor to check compliance;

(d) Publish and call for comments on any amendments to be made to the BMP-S; or

(e) Request a redraft of the BMP-S or a drafting of an entirely new BMP-S if the amendments are sufficient to warrant it.